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# The effect of chloroform upon the rotation in the internodes of Nitella[1]

SUSAN P. NICHOLS

(WITH PLATE 5 AND TWO TEXT FIGURES)

While experimenting on punctured *Nitella* cells, the writer has observed that, at the time when the puncture is made, the movement of the protoplasm does not always cease throughout the internode. Frequently the rate of movement at a distance from the wound is only slightly slowed down, the effect depending upon the manner in which the needle is handled. A quick thrust results in the immediate stopping of movement throughout the cell, while a steady pressure on a sharp needle until it penetrates the wall results in the cessation of movement at the wound and directly below it in the direction of the flowing protoplasm, but only slightly affects the movement in the remainder of the cell. When the needle is withdrawn the plastids and particles carried in the escaping protoplasm quickly plug the opening and stop the loss from the cell. Whether the movement ceases throughout the cell or not, the general process of recovery is the same. The protoplasm in the unaffected portion begins to move and the rate of this movement gradually increases until it is normal once more. When the moving protoplasm with its plastids and particles strikes the quiet cytoplasm at the wound, some of it comes to rest, while some slowly moves toward either side until it is caught and carried along in the normally streaming protoplasm.

The cytoplasm with the particles and plastids that have been stopped by the quiet area rapidly accumulates, until there is a dense crescentic mass piled up above the wound, with a stream of moving protoplasm on each side (fig. 1). The extent of the quiet area below the crescent and in the direction in which the protoplasm was flowing is indefinite, but usually by the aid of the denser streams at the sides it is possible to trace the area until it passes out of sight around the internode. This condition usually persists for several minutes.

When the puncture is made a few plastids may be broken from the wall layer and are then carried away in the moving cytoplasm. The plastids immediately below the plug may show some signs of injury, but no

[1] Paper No. 5, Botanical Laboratory, Oberlin College, Oberlin, Ohio.

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injury is shown by the plastids throughout the remainder of the quiet area. If the internode is returned to the culture glass and allowed to remain a few hours, it will be found that many of the plastids in the quiet area have left the wall and can now be seen floating in the streaming protoplasm. The area left free from plastids is frequently irregular in outline, especially in the lower portion (fig. 2).

If a radial longitudinal section (figs. 6, 7) is made while the protoplasm is massed above the puncture, it shows the mass of protoplasm extending into the central cavity of the cell and projecting slightly forward in the line of flow. This massed protoplasm shows a denser condition in the forward portion, suggesting the accumulation of particles when movement is checked. Just back of this dense region of massed protoplasm, where very slow movement can be still detected in the living material, the protoplasm takes a lighter stain and there are numerous small vacuoles pre-

Fig. 9. A tangential section passing under the puncture before movement has started in the area below the wound.

sent. The definite outline of this mass as it appears in section suggests that a membrane may be formed. On the opposite side of the cell, where the protoplasm is unaffected and movement is still normal, its surface is more uneven. This is even better shown in text figure 10.

The region above the wound through which the rate of movement is retarded is indicated by a thickening of the layer along the wall as shown at *a* in figures 6 and 7. This layer is not uniform in thickness, but every now and then a projecting mass of cytoplasm can be observed, as at *d* in figures 6 and 7. Some of the plastids which were broken from the wall when the puncture was made can be seen at *b* and *c*. If the section is made slightly tangentially to the wound, the mass of retarded protoplasm is better shown (text fig. 10).

After a time the protoplasm above and under (not below) the plug, and also the protoplasm at the margins of the quiet area begins to move slowly and this process continues until both have disappeared. The movement in this region does not regain its normal rate for some time, but gradually the rate increases until the entire body of protoplasm is flowing

normally again. A longitudinal section through this region made before the normal rate has been fully regained will show that the layer of protoplasm along the wall is, for some distance, much thicker than normal, as shown in figure 9. But this layer is in motion, and there is no indication of any increase in the density of the cytoplasm. It would seem as if the moving protoplasm piling up against the quiet area must exert considerable pressure upon the non-motile cytoplasm, but I have never observed this area start to move as a body. Rather, there is a gradual resumption of movement near the margins of the area, which would suggest that the pressure of the protoplasm did not play any important part in the re-establishment of movement.

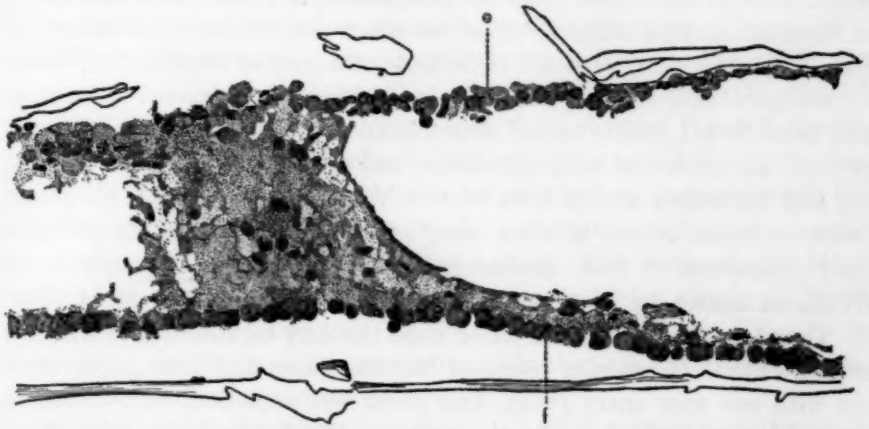

Fig. 10. A slightly tangential section, taken beneath the region of contact showing the massed protoplasm which has been blocked by the motile area at the point of contact. The plastids, which have loosened from the wall, are clearly shown, as well as the line that might suggest a plasmatic membrane over the surface.

In punctured *Chaetomorpha* (Nichols, 1923), which has a thick layer of non-motile protoplasm next to the wall, it has been possible to demonstrate the formation of a cell membrane which separates the injured protoplasm of the plug from the remainder of the cell. This membrane was completely formed in forty-five minutes or less, according to the severity of the injury. The formation of such a membrane in *Nitella* has not been detected, but it may have been formed about the plug without involving the quiet area. That such a membrane is formed is indicated by the fact that in a few days a new cell wall forms, separating the plug from the rest of the protoplasm. That this membrane does not extend over the quiet area is shown by the readiness with which movement is recovered in this region.

In my article on 'The Effect of Wounding upon the Rotation in the Internodes of Nitella' (Nichols, 1925), it was suggested that the loss of movement in the protoplasm at the wound might be due to the effect of some toxic substance formed from the injured protoplasm, and that this effect would naturally be more extensive in the direction of the flowing protoplasm, thus perhaps accounting for the quiet area below the puncture. When the puncture is made, any substance liberated would be carried along by the moving protoplasm, but this substance might not be uniformly distributed, and therefore, some rows of plastids might be more seriously injured than others. The gradual resumption of movement would then be dependent upon the disappearance of this toxic substance, or its neutralization. I have studied the effect of a series of solutions which have been previously reported to influence the rate of rotation in *Nitella*.

Kühne (1864) showed that ether and chloroform arrested streaming, and later Ewart (1903) stated that 'Solution in water of from 10 to 25 per cent saturation of both chloroform and ether at once retards streaming and ultimately causes it to cease without any quickening preceding death as often occurs in other cases'. Osterhout and Harris (1928) also used chloroform in their experiments on 'Protoplasmic Asymmetry in *Nitella* as Shown by Bioelectric Measurements.'

Therefore chloroform and ether were the first solutions with which I experimented. Triangular pieces of blotting paper and filter paper were cut with one very sharp point, this point was saturated with the solution, and then pressed against the wall of a *Nitella* internode. Absorbent cotton was rolled into a fine point and applied in the same manner. These methods proved unsatisfactory, since it was impossible to press the points against the wall firmly enough to make a good contact without affecting the entire adjoining portion of the internode, instead of a spot in the moving protoplasm. A capillary pipette was then used, and this proved very satisfactory, since it was possible to apply the solution to a very limited and definite area of any desired portion of the internode. For satisfactory results the pipette must be held at a right angle to the wall, to prevent, as far as possible, the spreading of the solution over the surface. The pipette was used free hand, as it was then possible to work much faster than by the use of a pipette holder, and equally good results were obtained. Before applying the solution, the water was drained from the slide, and a piece of blotting paper was passed along the sides of the material to remove any water adhering to it. After the pipette was withdrawn the material was washed in fresh water to remove any trace of the solution that might be adhering to the wall.

In studying a treated internode after movement had ceased, it was

difficult to be sure of the direction in which the protoplasm had been rotating at the time of the experiment. This was especially true in the sectioned material and, therefore, a definite place on the internode was selected for all applications. The portion of the internode in which the protoplasm was flowing away from the nearest node was always selected for the experiments. In later studies of that internode, it was always possible to be sure of the direction of the flow of the protoplasm at the time of the experiment, simply by determining the relation of the spot under observation to the nearest node.

When a pipette of ether is applied, movement does not cease immediately, and there is no visible effect upon the plastids, but if the contact is maintained for fifty or sixty seconds a gradual retarding of the moving particles will be noticed as they approach the region of contact. In the living material I have not been able to determine the limits of the affected area, for the influence of the ether seems to be diffused through the adjacent protoplasm, rather than to be limited to the region directly in contact with the pipette. The particles are checked as they approach the region of contact, and this checking of the movement results in an accumulation of protoplasm above the point of contact. This accumulation is not easily to be distinguished in the living internode, but is clearly shown in the killed and decolorized cell (fig. 4). On account of the difficulty in determining the limits of the affected area in the living internode the experiments with ether were discontinued.

When a pipette filled with chloroform is held in contact with the internode for five to ten seconds, movement will not cease for a second or more, and then movement ceases at the point of contact and in the region below in the direction in which the protoplasm is flowing, but not in the other portions of the internode. Thus a spot of non-motile cytoplasm is formed within the mass of moving protoplasm as a result of the action of the chloroform. In one or two cases movement throughout the entire cell ceased, but this was probably the result of carelessness in applying the pipette to the surface. Perhaps the pipette was pressed against the wall with too much force so that a mechanical shock resulted that might possibly account for the cessation of movement.

When the particles in the moving protoplasm come against the quiet chloroformed area, the result is similar to that observed after puncturing and after treatment with ether, i.e., the movement of the particles is stopped, while those a little to one side do not stop entirely but are checked in their movement and slowly pass around the sides of the affected area until they join the normally moving stream beyond. Thus this region is very soon well defined by a crescent of denser protoplasm formed by the

protoplasm that piles up against and above it (fig. 5). The extent of the quiet area below the region of contact is not definite, but it is usually possible to follow it until it disappears around the other side of the internode.

The plastids in the chloroformed area do not always show any effect from the treatment, but sometimes there is a slight difference in the transmission of light through this region, so that it appears slightly brighter than the remainder of the cell. Once or twice the application had been followed by a definite injury to the plastids, as shown by their change in appearance. In these cases the plastids appear darker and more widely separated from each other. This appearance might be brought about by a rounding up of the plastid bodies. Whether the plastids show any immediate effect or not, there is evidently some change in their condition, for if the internode is returned to the culture glass for twenty-four hours or more it will be found that most of the plastids in the treated area have left the wall and are to be seen floating in the stream of moving protoplasm. The loss of the plastids leaves a clear patch on the inside of the wall, as shown in figure 3. For several days these plastids can be recognized in the mass of flowing cytoplasm. The plastids in the quiet area below the actual region of contact do not show injury or leave the wall later.

Gradually that portion of the protoplasm of the quiet area which adjoins the streaming cytoplasm at its sides begins to move, while the protoplasm piled up above the arrested mass pushes slowly under the contact spot. The piled up protoplasm is fairly thick before this movement is started, and it seems as if it must exert considerable pressure on the quiet mass by the time movement begins (fig. 8). However, the quiet area was not moved as a whole in any of my experiments, but movement was resumed gradually at the margins, until finally the whole mass was streaming normally again.

If a radial longitudinal section (fig. 8) is made through the chloroformed area while the protoplasm is massed above, it shows the protoplasm projecting into the center of the cell, and protruding slightly over the upper margin of the quiet protoplasm.

The region through which the protoplasm is retarded above the quiet area is very clearly shown in figure 8. The concentration of the particles in the forward portion is more pronounced in this case than in the massed protoplasm of the punctured cell. Of cource the portion of the internode affected by the puncture, and therefore the amount of protoplasm piled up against the quiet area, is larger also.

If the pipette of chloroform is held in contact with the cell for a minute

or more movement does not cease during the application but evidently the injury is more serious than is indicated by the appearance of the internode, since such exposure is always followed by the death of the cell inside of six hours.

If the first application of chloroform is made at one end of the internode and, after rotation has been re-established, a second application is made at the other end of the cell, movement does not cease in the recovered area, and the process of recovery follows the usual course. Although movement is re-established throughout the internode after such a double application, the normal rate is never recovered fully. On the contrary, after a half hour or an hour, the rate of movement begins to grow slower and slower, until it finally ceases in three to six hours.

In order to learn whether the internode could recover from a more extensive treatment the end of the internode was dipped in chloroform and held there for two to five seconds. In all but one case no movement was visible after the internode had been washed; in that one case a very slow movement of the finer granules was visible, but there was no movement of the larger particles. At the end of an hour all movement had ceased, and there was no further recovery. In these experiments it was impossible to determine the portion of the internode that had been in contact with the chloroform, as the appearance of the entire internode indicated injury.

When a normal cell of *Nitella* is punctured, the opening is closed in a few seconds by a mass of denser protoplasm, plastids, and other particles, thus checking any further loss from the interior of the cell. Recovery of streaming follows in a few minutes, and thus the injury appears temporary. A puncture made within a chloroformed area is not followed by permanent recovery. The puncture may be closed by the formation of a plug, and movement may be present in the remainder of the cell for a time, but in a few hours the movement ceases and death follows.

The cessation of movement and the subsequent recovery of a chloroformed spot follows the procedure observed in the punctured cell so exactly that it seems as if in both cases the procedure must be the result of similar changes in the condition of the protoplasm. In the chloroformed cell no plug is formed that might impede movement. It would seem, therefore, that some change in the condition of the protoplasm directly in contact with the chloroform must occur which prevents movement.

The experiments of Brinley (1928), Edwards (1923), and Heilbrunn (1920) all show that dilute solutions of chloroform tend to decrease the viscosity of protoplasm, but Heilbrunn states that 'As the concentration of the anesthetic is increased the decrease in the cytoplasmic viscosity becomes more and more pronounced until a turning point is reached. At

this point gelation or coagulation occurs.' It seems probable that similar changes occur at the point of chloroform contact in the *Nitella* internode, since movement does not stop instantly, but only after one or two seconds. In the experiments on the *Nitella* internode only a small portion of the protoplasm was in contact with the solutions. Therefore, any change in condition, such as the formation of a lump of gel within the normal protoplasmic sol, would be limited in extent. This lump, as noted, is not carried along in the stream, and seems to be continuous with the motionless plasma membrane. I am making further studies of the action of other anesthetics and poisons on streaming protoplasm as bearing on the problems of cytolysis and shock effects.

I wish to express my appreciation to Professor R. A. Harper for his continued interest in the problem and for reading the manuscript.

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**Explanation of plate 5**

Fig. 1. Punctured internode with a mass of protoplasm above the puncture. Photographed 12 minutes after the puncture.

Fig. 2. Punctured internode 24 hours after the puncture was made External plug shown by dark shadow above center; loss of plastids from the parietal layer shown in clear portion below.

Fig. 3. Internode 24 hours after the application of chloroform. Clear portion the area of contact showing the loss of plastids from the parietal layer.

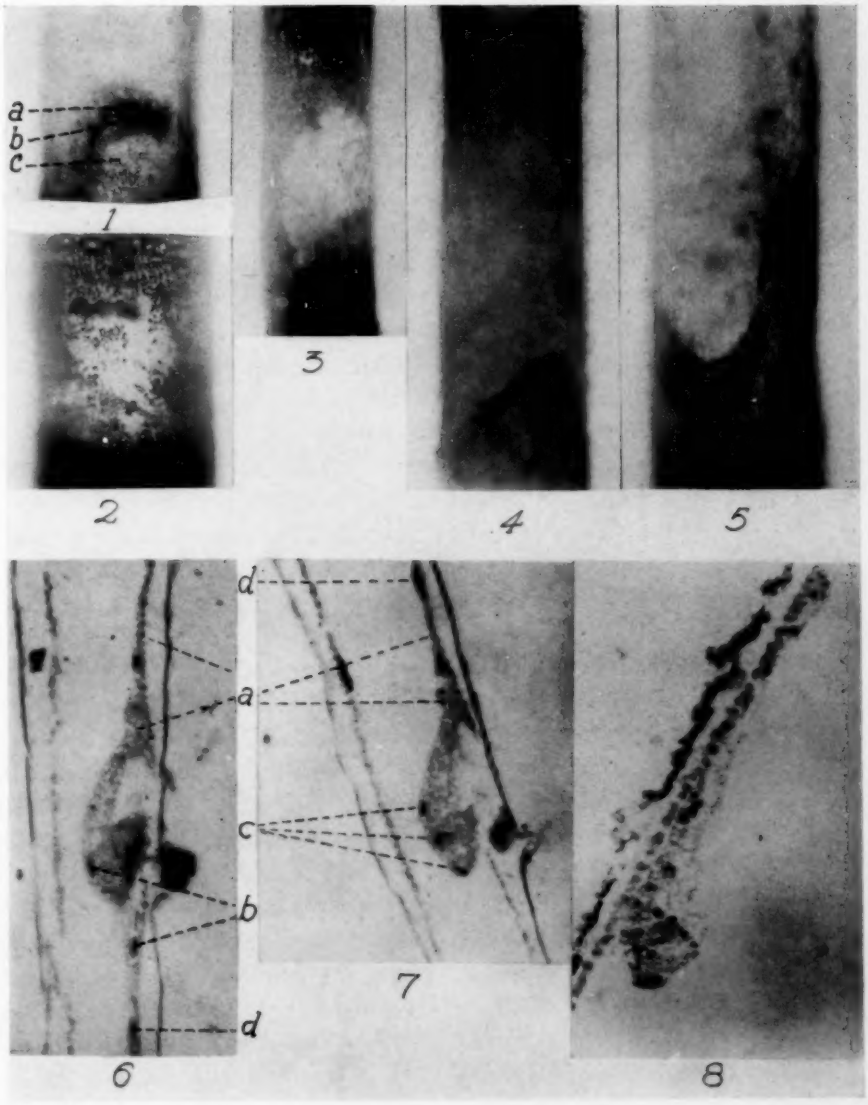
Fig. 4. Internode 30 minutes after the application of ether. Dark, crescentic shadow an accumulation of protoplasm a little above the area of contact.

Fig. 5. An internode 30 minutes after the application of chloroform.

Fig. 6. A radial longitudinal section through a punctured internode before movement under the plug has started.

Fig. 7. A radial longitudinal section through a punctured internode as movement under the plug is starting.

Fig. 8. A longitudinal section through an internode after movement below the wound has started but before it has regained the normal rate of movement.




NICHOLS: ROTATION IN NITELLA

UNIV OF MICH.

# The origin and development of the vegetation of Sandy Hook

M. A. Chrysler

(with a text figure and plates 6, 7)

Sandy Hook, a narrow peninsula about five miles long, extending northward from the coast of New Jersey, is a well-known feature of the landscape, for its lighthouse, erected in 1764 and therefore the oldest one in the United States, is visible from steamships approaching New York harbor. Its botanical interest is due to the fact that its acquirement by the U. S. Government in 1892 has preserved it from devastation by the summer colonists, and it represents the most northern of the relatively unaltered pieces of 'beach'[1] along the New Jersey coast. Moreover its flora differs from that of any other portion of the coastal strip, and the marked changes which in historic times have taken place in its extent provide a favorable field for a study in succession.

Among botanists who have studied the region is Britton, who in 1885 collected a number of plants which are filed in the herbarium of Rutgers University. Harshberger (1901, 1903) has described the features of the New Jersey strand flora, but apparently did not include the Hook in his investigations. For several years the writer has made frequent visits to the area at various seasons, and has been actively aided by members of the staff of officers of Fort Hancock, whose kind cooperation is here gratefully acknowledged.

A few facts concerning the history of Sandy Hook will show what great changes have occurred in its topography, and how recent must be some of its vegetation (Bache, 1845; Cook, 1885). It is the most northern extension of the line of beaches which guard the Jersey coast, and owes its formation chiefly to littoral currents, as do all of the beaches. In the case of the Hook however, the Navesink and Shrewsbury Rivers have played an important part; for prolonged periods they have emptied to the west of the Hook, but at times waves have broken through the beach and converted the Hook into an island, while at other times an isthmus connected the Hook with the adjacent Navesink Highlands (see map, fig. 1). These inconvenient changes have been checked by the construction in 1920-21 of a sea-wall along the eastern side of the south end of the Hook. Since the first survey in 1685 by Keith the peninsula has quadrupled in size. Since

[1] A *beach* in New Jersey means a narrow sandy strip of land bordering the coast, and in many cases separated from the upland by bays such as Barnegat Bay.

that time a number of surveys have been made, and from these we learn that the headland advanced north as follows:

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| From | 1779 | to | 1819, | 40 | years, | 540 | feet, | or | 13.5 feet per year |
| " | 1819 | to | 1836, | 17 | " | 1150 | " | " | 67.6 " " " |
| " | 1836 | to | 1842, | 6 | " | 630 | " | " | 105. " " " |
| " | 1842 | to | 1844, | 2 | " | 200 | " | " | 100. " " " |

These figures give an average advance of almost 40 feet per year. The site of Sandy Hook light was in 1764 almost on the point of the Hook; since then the point has made out to the north nearly a mile.

Even a brief visit to the region will show that the vegetation is quite different from that of the beaches in general, and if the approach is made from the adjacent Navesink Highlands, the contrast is again very striking. Instead of the shrubby thicket characteristic of Seaside Park or Surf City, or the oak-hickory forest covering the Highlands (Harshberger, 1910), we see a luxuriant growth of red maple, holly, and hackberry occupying what appears to be the oldest part of the area. It will be advisable however to describe first the communities which represent the initial stages in succession.

1. *Salt-marsh.* Several small but well-marked areas occur, of which the one on the inner side of the peninsula[2] known as Island Beach or Plum Island is typical. In water is a pure stand of *Spartina glabra* Muhl., var. *alterniflora* (Loisel.) Merr., just behind this a zone of *Suaeda americana* (Pers.) Fernald, with patches of *Salicornia ambigua* Michx.; and a few plants of *Limonium carolinianum* (Walt.) Britton. In places the second zone is replaced by *Iva oraria* Bartlett. Just at the edge of tide level occur two species of *Salicornia*, *S. ambigua* Michx. and *S. mucronata* Bigel., with *Spergularia marina* (L.) Griseb. This zone is closely followed by the middle beach, characterized by *Atriplex patula* L., var. *hastata* (L.) Gray (scarce here), *Cakile edentula* (Bigel.) Hook., *Spartina patens* (Ait.) Muhl., and other plants listed under the next heading. This community is thus quite characteristic of salt-marshes of the middle Atlantic region. In a depression behind a dune on Island Beach occurs an extended community of *Distichlis spicata* (L.) Greene; along the edge a few plants of *Aster tenuifolius* L. were found. Stone (1912) records the occurrence of *Pluchea camphorata* L., but such brackish-marsh plants as *Sabatia* and *Gerardia* have not been found, and *Hibiscus* occurs only in a marsh near the east side of the peninsula.

2. *Middle beach.* This broad zone, beyond the reach of summer waves is well developed at numerous places along both sides of the peninsula.

[2] In recent years a sand bar has converted into a peninsula what is shown on the older maps as an island.

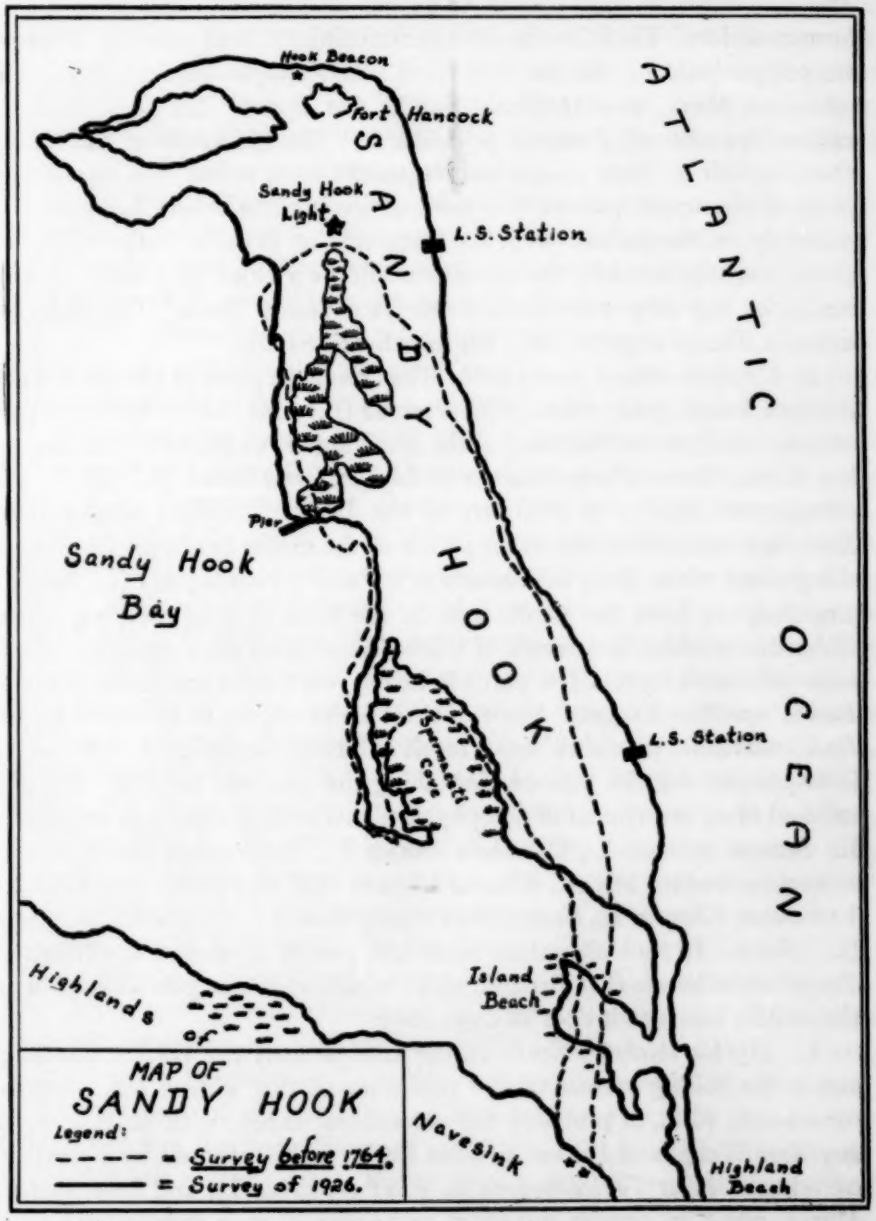



Fig. 1. Outline map of Sandy Hook, showing William Lawrence's survey made prior to 1764, and U. S. Coast and Geodetic Survey of 1926. Courtesy of New Jersey Dept. of Conservation and Development, and of U. S. Coast and Geodetic Survey.

The vegetation is sparse in most places except where *Spartina patens* forms a society. The following are characteristic: *Cakile edentula, Euphorbia polygonifolia* L., *Salsola Kali* L., *Solidago sempervirens* L., *Xanthium echinatum* Murr., and *Atriplex patula* L., var. *hastata* (L.) Gray, with occasional patches of *Arenaria peploides* L. The thickness of the leaves characteristic of these plants has frequently been noted. An interesting plant of the upper part of this zone, *Artemisia Stelleriana* Bess., occurs sparingly in comparison with its frequency at Seaside Park. The list given here is practically the same as would be yielded by a study of any beach for say fifty miles southward from Sandy Hook. Compare for instance, Harshberger's (1901) list from Seaside Park.

3. *Upper beach and young dune.* The dominant plant of this zone is the common beach grass, *Ammophila arenaria* (L.) Link, which here occupies some areas of the southern end of the Hook almost exclusively, building up low dunes. Several large patches of *Lathyrus maritimus* (L.) Bigel. are conspicuous objects in this part of the Hook. *Solidago sempervirens, Xanthium echinatum,* and other plants of the upper beach persist among the grasses, while along the eastern side *Psedera quinquefolia* (L.) Greene stretches out from the shrub zone in the form of long creeping cords. Older dunes which are devoid of thicket vegetation show masses of *Hudsonia tomentosa* Nutt. a few yards in extent, with some scattered plants of *Lechea maritima* Leggett. Some of these areas appear to be covered with *Hudsonia* rather than shrubs as a result of human disturbance. This factor is responsible for the introduction along the concrete roadway and the railroad of an assortment of xerophytic plants such as *Cenchrus tribuloides* L., *Bromus tectorum* L., *Oenothera biennis* L., *Trichostema lineare* Walt., *Artemisia caudata* Michx., *Linaria vulgaris* Hill, *Saponaria officinalis* L., *Verbascum Thapsus* L., *Gnaphalium obtusifolium* L., *Polygonella articulata* (L.) Meisn. In such situations occur also poorly developed specimens of *Strophostyles helvola* (L.) Britton, which is here unable to gain a foothold on the middle beach as it does at Cape May.

4. *Myrica thicket.* North of the treeless area the thicket stretches across the rolling surface of the peninsula as this widens out. *Myrica carolinensis* Mill., is probably the commonest shrub, with much *Prunus maritima* Wang. and *Prunus serotina* Ehrh., and overgrown by a plentiful covering of *Rhus Toxicodendron* L. *Rhus copallina* L., and *Rosa humilis* Marsh. occur in smaller quantity, and some *Psedera quinquefolia* finds support on the shrubs. There are also young specimens of *Juniperus virginiana* L. Conditions are severe, as is evidenced by the wind-blown appearance and spreading habit of the shrubs.

Depressions in this area are generally occupied by *Phragmites communis*

Trin., with *Baccharis halimifolia* L. along the edge. In autumn these spots present a beautiful appearance on account of the plume-like inflorescences.

Further north the cedars are older, and are struggling with the almost continual winds; most of the trees are leafless except the wisp-like tips, while some have given up the battle. A few young *Ilex opaca* Ait. appear in the thicket area.

Some good examples of dunes of medium age occur on the west side (see fig. 2). The summit is covered by the thicket, with a few wind-blown cedars and cherries projecting at the middle of the group. Surrounding this is generally a fringe of *Hudsonia tomentosa*, and *Lechea maritima*. Occasional plants of *Convolvulus sepium* L. and *Teucrium canadense* L. occur in this marginal zone, and a few *Solidago sempervirens* are able to endure the dry conditions. These dunes present a striking appearance for a short time in May, while the beach plum is covered with its creamy white flowers. Certain of the smaller dunes are entirely covered by *Prunus maritima*, *Prunus serotina*, and *Rhus Toxicodendron*.

5. *Maple-holly forest.* The oldest dunes, extending north and west from the thicket, are densely covered with a strikingly mesophytic looking growth made up of large specimens of *Acer rubrum* L., *Ilex opaca* (some over one foot in diameter), *Juniperus virginiana*, *Prunus serotina*, *Celtis occidentalis* L.—in many places densely clad with a mantle of *Rhus Toxicodendron* and *Psedera quinquefolia*, which reach the tree-tops—and smaller numbers of *Menispermum canadense* L., *Vitis cordifolia* Michx., *Smilax rotundifolia* L., *Celastrus scandens* L., and *Polygonum scandens* L. Where the forest is not dense, and especially on the edge of clearings, *Rhus copallina* L., *R. glabra* L., and *R. typhina* L. are common, with *Rosa humilis* Marsh. in smaller numbers, while in the more moist or shady parts *Cornus florida* L., *Viburnum dentatum* L., *Vaccinium corymbosum* L. (apparently the only ericad on the Hook), *Pyrus arbutifolia* (L.) L.f., *Ilex verticillata* (L.) Gray, and *Sambucus canadensis* L. have been observed. The herbaceous growth includes: *Solanum Dulcamara* L., *Eupatorium urticaefolium* Reichard, *Solidago rugosa* Mill., *Smilacina stellata* (L.) Desf., and *Geranium Robertianum* L., which ventures even out to the road-side. The occurrence of the last two, of relatively northern range, on the Jersey beaches, has been discussed by Stone (1912, p. 105). Along roadways *Opuntia vulgaris* Mill., *Rubus villosus* Ait., *R. occidentalis* L., and *Oenothera biennis* L. are occasional, with an abundance of *Bidens bipinnata* L., and numerous 'weeds' such as *Lepidium virginicum* L., *Nepeta cataria* L., *Achillea Millefolium* L., *Rumex crispus* L., several clovers, etc.

The composition of the forest varies more or less; the northern portion of this area is higher and appears to carry the oldest vegetation of the

Hook, with *Acer* and *Celtis* as dominants, with much *Prunus serotina*, and a heavy mantle of lianas, but with comparatively little *Ilex opaca*. Slightly further south there is less maple but much holly a foot in diameter, with considerable cedar. At the north end of the maple-holly area the forest drops off quite suddenly, bounded by a broad depression covered by *Phragmites*, north of which is the settled area of Fort Hancock. It is quite possible that the topography has here been altered artifically. The northern extremity of the forest shows no maples and but little holly, and consists of cedar, cherry, hackberry and a little black locust, *Robinia pseudo-Acacia* L., all suffering from strong winds (see fig. 4). A lower zone consists of the four species of *Rhus*, with some beach plum. Flanking this society is the thicket in which *Myrica carolinensis* dominates, mixed with *Prunus maritima*, *Rhus copallina*, and a few *Myrica asplenifolia* and *Rosa humilis*. *Smilacina stellata* persists under the cedars, and in the thicket there is a good deal of *Solidago sempervirens*.

Two other areas deserve attention. One of these is a fresh marsh lying to the east of the maple forest. Oil has recently been applied to this marsh, destroying some of the plants, but it is still possible to determine the presence of several plants which are absent or rare on other parts of the peninsula. *Phragmites* appears to be the commonest grass in the depression, occurring mixed with *Typha latifolia* L., while near the margin occur a few plants of *Hibiscus Moscheutos* L. In a slightly higher zone is to be found the only fern of the area, *Thelypteris palustris* (Salisb.) Schott, var. *pubescens* (Lawson) Fernald.[3] On the west side of the maple-holly forest occur the only pines so far discovered on the Hook. These are three specimens of *Pinus rigida* Mill., forming a group somewhat separated from the maples by thicket. These pines are about forty feet high and are well supplied with cones, so it is not easy to explain why there should not be other groups. It will be interesting to trace the further history of this small colony.

Before considering the probable development of the vegetation, it will be well to examine into its sources and the available methods of dispersal. It must be borne in mind that the beach just south of Sandy Hook, lying between the ocean and the Shrewsbury River, is extremely narrow for a distance of several miles, averaging not more than 500 feet. It is quite improbable that this narrow stretch ever bore arboreous growth, but it must have been covered by dune and perhaps thicket societies. Moreover the Hook has been connected with the adjacent Navesink Highlands by means of shifting sand-bars during part of its existence. For the rest of the time it has been an island. The geologists in fact insist that the ridge bear-

[3] Fernald in Rhodora 31: 34. 1929.

ing the maple-holly forest was a submarine formation (Cook, 1885, p. 76). They call attention to the proportion of glauconite (as much as 20 per cent), and the stratification of this area. The view seems tenable that the dune and thicket elements of the flora have been derived from the beaches to the south of the Hook, while the trees have been almost entirely derived from the adjacent Highlands. In order to test this view, table 1 has been drawn up, on the basis of the writer's observations, checked up by comparison with Harshberger's record.

TABLE I

*Vegetation of Sandy Hook and other regions compared*

| NAME OF PLANT | SANDY HOOK | NAV. HIGHLANDS | SEASIDE PARK |
|---|---|---|---|
| *Forest* | | | |
| Pinus rigida | (+) | + | + |
| Juniperus virginiana | ++ | + | + |
| Acer rubrum | ++ | + | – |
| Ilex opaca | ++ | + | + |
| Robinia pseudo-Acacia | + | + | – |
| Celtis occidentalis | ++ | + | – |
| Prunus serotina | ++ | + | – |
| Quercus prinus | – | ++ | – |
| Quercus alba, Q. rubra | – | + | – |
| Quercus ilicifolia | – | – | + |
| Castanea dentata | – | + | – |
| Carya spp. | – | + | – |
| Liriodendron Tulipifera | – | + | – |
| Betula populifolia | (+) | + | – |
| Cornus florida | + | + | – |
| Viburnum dentatum | + | + | – |
| Rhus Toxicodendron | ++ | + | + |
| Psedera quinquefolia | ++ | + | + |
| Smilax rotundifolia | + | + | + |
| Menispermum canadense | + | + | – |
| Vitis spp. | + | + | – |
| *Thicket* | | | |
| Myrica carolinensis | ++ | + | ++ |
| Prunus maritima | ++ | – | ++ |
| Rhus copallina | ++ | + | + |
| Rhus typhina | + | + | + |

Note: + indicates present
++ " very common
(+) " very rare
– " not found

*Quercus* spp., *Castanea*, *Carya* spp., *Liriodendron*, while not occurring on the Hook, have been introduced into the table in order to bring out the contrast in the vegetation of the Hook and the adjacent Highlands. With reference to *Pinus*, *Juniperus*, and *Ilex*, the narrowness of the strip of beach immediately south of the Hook must be kept in mind; since all of these occur on the neighboring mainland, it is probable that all came from

here. Most of the shrubs and climbers may have had their origin in either mainland or beach. *Menispermum*, however, does not appear to grow on the beaches, and *Vitis* is rare in such situations.

An inspection of the table at once suggests that the mainland has supplied most of the trees, also that birds have been the agents of dispersal for most of the seeds, the exceptions to this being *Pinus*, *Acer*, *Robinia*, and perhaps *Betula*.[3] But it is not necessary to fix the responsibility on the birds without evidence. Forbush (1905) has made an extended study of the foods used by birds, and has listed the most important fruit-bearing trees furnishing food for birds; these are indicated as '1' in table 2, while the fruit-bearing plants of less importance to birds are

TABLE 2

*Probable carriers of seeds to Sandy Hook*

| PLANTS ON SANDY HOOK | POSITION OF FRUIT IN FORBUSH'S LIST | EATEN BY: |
|---|---|---|
| Juniperus virginiana | 1 | yellow-throated vireo (F), cedar wax-wing (F), robin (B) |
| Ilex opaca | 2 | robin (F) |
| Celtis occidentalis | 1 | cat bird (H), robin (B), blue bird (B) |
| Prunus serotina | 1 | wood thrush (F), grouse (F), robin (F) |
| Cornus florida | 1 | red-eyed vireo (F), blue jay (B), robin (B) |
| Vaccinium corymbosum | 1 | red-eyed vireo (F), robin (B), bluebird (B) |
| Berberis vulgaris | 1 | robin (B) |
| Amelanchier canadensis | 1 | cedar wax-wing (H), rose-breasted gros-beak (M), robin (B) |
| Rubus villosus (et. al.) | 1 | wood thrush (F), red-eyed vireo (F), robin (B) |
| Sambucus canadensis | 1 | rose-breasted grosbeak (M), blue jay (B) |
| Rhus toxidodendron | 2 | robin (F), downy woodpecker (H), red-bellied woodpecker (B) |
| Psedera quinquefolia | 1 | grouse (F), red-bellied woodpecker (B), robin (B) |
| Smilax rotundifolia | 1 | robin (F), cat-bird (H) |
| Menispermum canadense | 2 | —— |
| Vitis spp. | 2 | red-eyed vireo (F), robin (F), grouse (F) |
| Celastrus scandens | 2 | grouse (F) |
| Myrica carolinensis | 1 | chickadee (F), myrtle warbler (H), tree swallow (H) |
| Prunus maritima | 2 | —— |
| Rhus glabra, R. typhina | 1 | chickadee (F), grouse (F), robin (F) |
| Rosa humilis | 2 | grouse (F) |
| Phytolacca decandra | 2 | grouse (F) |

Note: Capital letters indicate authority quoted from literature list on page 173, thus:

B indicates Beal (1897, 1915, or 1922)
F " Forbush (1905)
H " Hausman (unpublished)
M " McAtee (1908)

indicated as '2'. He also furnishes a list of the fruits eaten by particular birds, based on stomach contents; this list is the basis of column three of

[3] Forbush (1905) finds seeds of birch and alder in the stomach of the rose-breasted grosbeak.

table 2, although I have fortunately had the advantage of the field experience of my colleague Professor L. A. Hausman, who has very kindly added to Forbush's list from his personal observations. It is a pleasure to acknowledge at this point my indebtedness to Dr. Hausman. All of the birds named in column three are at least summer residents of this region, as has been ascertained by reference to the work of Griscom (1923). The table clearly shows how large a share birds have had in the work of populating the Hook with plants. It now becomes apparent why trees with heavy seeds, such as oaks, chestnut, and hickories are absent from the Hook, although these are dominant trees of the Navesink Highlands; other reasons than difficulty of dispersal will be offered later. As in most other cases of plant distribution, there are puzzles. For instance, why are there only three pine trees, but hundreds of maples, when the disseminules are so similar, and a supply of both available? Why has *Betula populifolia* been so late in appearing? How was *Robinia* introduced? Why are *Sassafras* and *Nyssa* absent?

The mesophytic aspect of the forest, with its full-grown hardwoods and abundant lianas, comes as a surprise to all who visit this region. This aspect is, however, more apparent than real. *Juniperus* and *Ilex* are able to endure much wind and salt air, and the latter is regarded by Gifford (1900) as 'a dune-tree par excellence.' This writer calls attention to the close and jagged limbs of the coastal trees, in contrast to the pyramidal, symmetrical holly trees of the inland open field. Seven-mile Beach, near Avalon, formerly bore a forest of much the same composition as that of Sandy Hook, with the addition of a few oaks and some *Nyssa*.

An opportunity was recently afforded to calculate the rate of growth of the hollies of Sandy Hook, when several trees were felled in order to clear the way for a line of electric wires. Through the kindness of the Commanding Officer of Fort Hancock, disks were cut from near the base of two trees. After these were brought to the laboratory the surfaces were smoothed off, and the growth rings counted. The first tree had a diameter of 11.5 inches and showed 77 rings, while the other tree had a diameter of 13 inches and showed 96 rings. It is obvious that it takes a holly nearly a century to attain a diameter of a foot, under the conditions prevailing on the Hook. It may be that the forest is not very old; this view is supported by the absence of oaks, which we have seen are abundant on the Highlands.

With respect to the probable succession of vegetation on the area, the clearest sere is the one beginning with the beach-dune community, and passing through the thicket stage to the maple-holly forest. The pioneers here are *Cakile*, *Euphorbia polygonifolia*, *Xanthium*, *Salsola*, followed by *Ammophila*, *Lathyrus*, *Hudsonia*, and *Artemisia Stelleriana*. All four of

these may function as sand-binders. At a later stage the dunes are invaded by *Myrica*, *Prunus maritima*, *Rosa*, *Rhus Toxicodendron*, and *Psedera*. The first tree to gain a foothold is *Juniperus*, seedlings of which are scattered through the thicket area. As the cedars raise their heads above the shrubs, they are subjected to the strong winds which kill some and reduce the others to mere skeletons carrying bunches of leafy branches at their tips. Judging from the occurrence of *Prunus serotina* mixed with cedars on the summit of small dunes, the cherry is the next tree to become established. *Celtis* and *Ilex* appear to follow the cedars and cherries, and at about this stage climbers such as *Rhus Toxicodendron*, *Psedera*, and *Smilax* are able to reach nearly to the tree-tops. Latest of all come the maples, with the mesophytic vegetation forming lower layers, including *Cornus*, *Viburnum*, *Vaccinium*, *Berberis*, also climbers such as *Vitis* and *Menispermum*.

The question raised by this somewhat unusual sere is as to the probable future of the maple-holly forest. The area occupied is unfortunately small, and chances for disturbance are considerable, in spite of the protecting influence of the United States Government. Is this forest to be regarded as a climax of any kind? In his second paper on the New Jersey strand flora Harshberger (1903) speaks of a 'culminating stage,' constituted by the mesophytic thicket occupying depressions in the dune complex and characterized by the following flora: *Pinus rigida* Mill., *Sassafras*, *Vaccinium corymbosum* L., *Juniperus*, *Chamaecyparis*, *Myrica*. A second list is offered containing: *Ilex opaca* Ait., *Juniperus*, *Prunus maritima* Wang., *Rhus radicans* L., and *Solidago*. Perhaps Harshberger did not mean the word 'culminating' to be taken too literally; at anyrate the forest on Sandy Hook has passed beyond either of the stages represented by these lists. I should regard the community at Avalon as representing a more advanced condition than these so-called culminating stages. Judging from the invasion of the beach by oaks in the southern part of the state, it would appear that another stage might eventually be reached, for there is an abundant supply of seeds of oaks and hickories within easy distance of Sandy Hook, if these could be carried across, and if they could establish themselves. The scarcity of blueberries (restricted to a few individuals of one species, *V. corymbosum*) and entire absence of *Gaylussacia*, which is abundant on the Highlands, although these are readily eaten by birds, would indicate that at present some conditions of the soil are unfavorable. It may be suggested that the suitable soil fungi are absent, and this in turn may be due to insufficient supply of humus or to unsuitable soil reaction. On the whole, the region seems not yet to have passed a xero-mesophytic stage.

SUMMARY

1. The changes in the configuration of Sandy Hook are traced, referring specially to the connections of the peninsula with the mainland.

2. The following communities are described: salt-marsh, beach and young dune, *Myrica* thicket, maple-holly forest.

3. The composition of these communities indicates that:

(1) Salt-marsh, beach and young dunes have a flora entirely similar to that of neighboring areas of the 'beach.'

(2) The thicket also resembles those of beaches for some distance south, although members of its flora occur also on the adjacent mainland.

(3) The forest contains no elements that are not also found in the neighboring Navesink Highlands, but lacks the oaks, chestnuts and hickories which are dominant on the latter. It is, on the contrary, a fairly mesophytic society made up of *Acer rubrum* L., *Ilex opaca* Ait., *Celtis occidentalis* L., and *Prunus serotina* Ehrh., with many climbers.

4. The conclusion is reached that birds have been the agents active in transporting the seeds of the plants of the forest area and thicket.

5. The probable stages in development of the forest are traced.

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## List of plants collected or observed

Note: plants marked (B) were collected by Britton, and those marked (C) by Chrysler. In both cases the specimens are preserved in the Herbarium of Rutgers University. The unmarked plants are from the author's lists. Mr. Percy Wilson and other members of the staff of the New York Botanical Garden have kindly aided in the identification of certain of the plants.

### Filicales

Thelypteris palustris pubescens (Lawson) Fernald (B), (C)

### Gymnospermae

Pinus rigida Mill.
Juniperus virginiana L. (C)

### Monocotyledoneae

Typha latifolia L.
Ammophila arenaria (L.) Link (B)
Andropogon scoparius L. (B)
Aristida tuberculosa Nutt. (B), (C)
Bromus tectorum L. (C)
Cenchrus tribuloides L.
Dactylis glomerata L. (C)
Distichlis spicata (L.) Greene (B)
Elymus virginicus L. (B)
Eragrostis pectinacea Gray (B), (C)
Eragrostis pilosa (L.) Beauv. (B)
Panicum amarum minor Vasey & Scribner (Ruger)
Panicum clandestinum L. (B)
Panicum virgatum L. (B), (C)
Phleum pratense L.
Phragmites communis Trin. (C)
Poa compressa L. (C)
Spartina glabra alterniflora (Loisel.) Merr. (C)
Spartina juncea Willd. (B)
Syntherisma sanguinale (L.) Dulac. (C)
Cyperus diandrus Torr. (B)
Cyperus Grayii Torr. (B), (C)
Cyperus strigosus L. (B)
Sciprus americanus Pers. (B)
Juncus dichotomus Ell. (B)
Allium vineale L. (C)
Asparagus officinalis L.
Smilacina stellata (L.) Desf. (C)
Smilax rotundifolia L. (B)

### Dicotyledoneae

Populus grandidentata Michx. (C)
Populus deltoides Marsh. (C)
Salix alba L.
Myrica asplenifolia L.
Myrica carolinensis Mill. (C)
Betula populifolia Marsh.
Celtis occidentalis L. (C)
Polygonella articulata (L.) Meisn. (B), (C)
Polygonum acre H B K. (B)
Polygonum prolificum (Small) Robinson (B)
Polygonum scandens L. (B)
Rumex Acetosella L. (C)
Rumex crispus L. (C)
Atriplex patula hastata (L.) Gray (C)
Chenopodium leptophyllum Nutt. (B)
Cycloloma atriplicifolium (Spreng.) Coulter (C)
Salicornia ambigua Michx. (B)
Salicornia mucronata Bigel. (Kelley)
Salsola Kali L. (C)

Salsola Kali tenuifolia G. F. W. May. (C)
Suaeda americana (Pers.) Fernald
Amarantus retroflexus L. (B)
Phytolacca decandra L.
Arenaria perploides L. (C)
Arenaria serpyllifolia L. (C)
Saponaria officinalis L. (C)
Silene antirrhina L. (C)
Spergularia marina (L.) Griseb. (C)
Ranunculus abortivus L.
Menispermum canadense L. (B), (C)
Berberis vulgaris L. (C)
Arabis lyrata L. (C)
Cakile edentula (Bigel.) Hook. (B)
Lepidium virginicum L. (C)
Amelanchier candensis (L.) Medic. (C)
Fragaria sp.
Prunus maritima Wang.
Prunus serotina Ehrh. (C)
Pyrus arbutifolia (L.) L. f.
Pyrus Malus L.
Rosa rubiginosa L. (C)
Rosa humilis Marsh. (C)
Rubus occidentalis L.
Rubus procumbens Muhl. (C)
Rubus villosus Ait.
Lathyrus maritimus (L.) Bigel. (B), (C)
Medicago lupulina L. (C)
Melilotus officinalis (L.) Lam. (C)
Robinia pseudo-Acacia L.
Strophostyles helvola (L.) Britton (C)
Trifolium hybridium L. (C)
Trifolium pratense L. (C)
Oxalis corniculata L. (C)
Geranium Robertianum L. (B), (C)
Euphorbia polygonifolia L. (B)
Rhus copallina L.
Rhus glabra L. (C)
Rhus Toxicodendron L.
Rhus typhina L.
Ilex opaca Ait. (B), (C)
Ilex verticillata (L.) Gray
Celastrus scandens L. (C)
Acer rubrum L.
Acer rubrum tridens Wood
Psedera quinquefolia (L.) Greene (B)
Vitis aestivalis Michx. (C)
Vitis cordifolia Michx. (C)
Hibiscus Moscheutos L. (C)
Hypericum mutilum L. (B)
Hudsonia tomentosa Nutt. (B)
Lechea maritima Leggett (B), (C)
Opuntia vulgaris Mill. (C)
Oenothera biennis muricata (L.) Link (B)
Daucus Carota L.
Ptilimnium capillaceum (Michx.) Raf. (C)
Cornus florida L. (C)
Vaccinium corymbosum L. (C)
Limonium carolinianum (Walt.) Britton (C)
Asclepias syriaca L.
Convolvulus sepium L. (C)
Myosotis sp.
Leonurus cardiaca L.
Nepeta cataria L. (C)
Prunella vulgaris L.
Teucrium canadense L.
Trichostema lineare Walt.
Solanum Dulcamara L. (C)
Linaria canadensis (L.) Dumort. (C)
Linaria vulgaris Hill (C)
Verbascum Thapsus L.
Veronica officinalis L. (C)
Martynia louisiana Mill. (B)
Plantago lanceolata L. (C)
Diodia teres Walt.
Galium aparine L. (C)
Galium Claytoni Michx. (C)
Galium pilosum Ait. (B)
Lonicera japonica Thunb. (C)
Sambucus canadensis L. (C)
Viburnum dentatum L. (C)
Viburnum molle Michx. (B)
Achillea Millefolium L.
Ambrosia artemesiifolia L. (C)
Artemisia caudata Michx. (B), (C)
Artemisia Stelleriana Bess. (B), (C)
Atser tenuifolius L.
Aster divaricatus L. (C)
Baccharis halimifolia L. (B), (C)
Bidens bipinnata L.
Bidens laevis (L.) B S P (B)
Chrysanthemum Leucanthemum L. (C)
Cichorium Intybus L.

Erigeron annuus (L.) Pers. (C)
Erigeron canadensis L. (B)
Eupatorium perfoliatum L. (B)
Eupatorium urticaefolium Reichard (C)
Gnaphalium obtusifolium L. (B)
Hieracium florentinum All. (C)
Iva oraria Bartlett (B)
Lactuca canadensis L. (C)
Lactuca integrifolia Bigel. (B)
Solidago Elliottii T. & G. (C)
Solidago rugosa Mill.
Solidago sempervirens L. (C)
Xanthium echinatum Murr. (C)

## Explanation of plates 6, 7

PLATE 6

Fig. 2. Low dune on west side of Sandy Hook. Highest part covered by *Juniperus virginiana* and *Prunus serotina*, surrounded by *Myrica carolinensis*. 23 March 1928.

Fig. 3. An older dune than the preceding. On high ground *Juniperus* and *Prunus serotina;* in front of these *Myrica* and *Prunus maritima;* foreground *Hudsonia tomentosa* and *Lechea maritima* with one group of *Solidago sempervirens*. 21 Oct. 1927.

PLATE 7

Fig. 4. Near north end of wooded area, showing *Celtis*, with *Prunus serotina* and some *Rhus copallina* in front of this. 21 Oct. 1927.

Fig. 5. *Ilex opaca* and *Acer rubrum* in the wooded region. Many trees are one foot in diameter. 23 March 1928.

CHRYSLER: VEGETATION OF SANDY HOOK

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CHRYSLER: VEGETATION OF SANDY HOOK

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## Notes on Pteridophyta from Mount Roraima

ALBERT C. SMITH

(WITH PLATE 8)

A recent collection made by Mr. G. H. H. Tate on Mount Roraima, British Guiana,[1] discloses several ferns of exceptional interest. In the present paper those considered noteworthy are discussed, and notes are added when previous descriptions seem incomplete.

HYMENOPHYLLOPSIS DEJECTA (Baker) Goebel. There is a complete morphological description of this remarkable species by Goebel (Flora **124**: 3–21. *f.1–10*. 1929). The specimen collected by Mr. Tate (no.445) on the summit of Mount Roraima agrees with this in morphological details, but is considerably larger than the specimens previously known. The following notes may be considered in connection with other mention of the plant:

Stipes usually 3 or 4 to a plant, 10–15 cm. long; fronds oblong, 10–20 cm. long, 5–7 cm. broad, the ultimate segments not exceeding 3 mm. in width.

PTEROZONIUM CYCLOPHYLLUM (Baker) Diels. This species also is discussed in morphological detail by Goebel (op. cit. 25–31). The specimen collected by Mr. Tate (no. 415) is a very robust one, the following description of which may be considered in connection with other notes on the species:

Caudex erect, stout (nearly 1 cm. in diameter), densely paleaceous, the scales castaneous, piliform, 5–7 mm. long, made up of 15–20 cells; stipes caespitose, castaneous below, olivaceous above, stout (about 1.5 mm. in diameter), glabrous except towards the base where there are a few scattered hairs similar to those of the caudex, up to 30 cm. long; lamina thick coriaceous, oblong, 3–4 cm. long, 1.5–2 cm. broad, the base cuneate, the apex rounded, the margins entire and stiffly revolute; venation flabellate, immersed, veins forking two or three times, about 36 at their termination (1 mm. or more from the margin ); sori 6–8 mm. long, occupying the ultimate portions of the veins; sporangia somewhat obconical, about .8 mm. on the long axis, cells of the annulus large and thick-walled, stalk short (not exceeding .3 mm. in length); paraphyses 1–1.5 mm. long, of 6–12 cells.

[1] Dr. H. A. Gleason has recently published an account of the angiosperms of the Tate Collection (Bull. Torrey Club **56**: 391–408. 1929), and reference may be had to his paper for a general description of the collection and the Mount Roraima region.

SYNGRAMMA ELAPHOGLOSSOIDES (Baker) Diels. This interesting plant is known from several collection numbers; the specimen which Mr. Tate collected (no. 437), from the summit of the mountain is a very robust plant. The following notes may be taken as supplementary to the original description:

Caudex subrepent, stout (up to 1 cm. in diameter), lignose, densely paleaceous, the scales castaneous, lanceolate from an oblong base, 6–7 mm. long, about 7 mm. broad at the base, the margins faintly serrate, the cells in 8–12 longitudinal series with thick dark brown partition walls; stipes crowded (about 3 per centimeter of caudex), up to 33 cm. long, stout (2 mm. or more in diameter); costa of the lamina canaliculate above, very conspicuous beneath, veins arising singly or in pairs, simple or forked, plane on both surfaces or slightly depressed beneath, 10 to 14 per centimeter near the margin; sori occupying about two-thirds the length of the veins, leaving a marginal band of 3–4 mm.

**Syngramma brevifrons,** n. sp.

Caudex short-repent, stout (about 5 mm. in diameter), lignose, densely paleaceous, the scales castaneous, lanceolate-acuminate from an oblong base, 4–6 mm. long, about .7 mm. broad at the base, the cells in 6–10 longitudinal series with thick dark brown partition walls, the apex often elongated into a pilose tip; stipes crowded (about 5 per centimeter of caudex), 8–12 cm. long, slender (about 1 mm. in diameter), olivaceous or castaneous, naked; lamina thick coriaceous, triangular-ovate, 3–4.5 cm. long, 2.5–3.5 cm. broad, cordate or rarely truncate at the base, rounded at the apex; venation pinnate, the costa canaliculate above, prominent beneath, the veins obscure, wide-spreading, arising singly or in pairs, simple or once-forked, plane above, depressed beneath, 12 to 16 per centimeter near the cartilaginous margin in which the ends are immersed; sori linear, occupying nearly the entire length of the veins, covering the lower surface of the lamina except for a costal and marginal band of about 1 mm.; sporangia about .5 mm. on the long axis, sometimes associated with a fine yellow powder.

Type, *Tate 421,* collected on the summit of Mount Roraima, British Guiana, 26 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. This fern may be placed in the section Austrogramme Fourn. with *S. elaphoglossoides,* the only other species of this alliance. The present species is the smaller and more slender in habit of the two, differing in morphological details as well. The scales of the caudex, in the present species, have an acuminate, sometimes pilose tip, which is less pronounced in *S. elaphoglossoides.* A consistent difference in the shape of the lamina is apparent—that of *S. elaphoglossoides* is lanceolate and several times as long as broad, while that of the smaller species is triangular-ovate and not

much longer than broad. The proportion of the stipe to the lamina is also consistent— in the former species the stipe is rarely twice as long as the lamina, while in the latter it is habitually two or three times as long. Perhaps the most important difference is in the proportionate length of the sori—in *S. elaphoglossoides* they are about two-thirds the length of the veins, leaving a marginal band of some width; in the present species they are practically as long as the veins so that the marginal band is inconspicuous.

POLYPODIUM MOLLISSIMUM Fée. The specimen collected by Mr. Tate (no. 501) agrees excellently with the description and plate of Fée (11 Mem. 47. *pl. 12, f. 2.* 1886). *P. mollissimum* is a species distinguished from others of its group by its small rhizome, short stipe, simple venation, soft pubescence below the pinnae, and setose sporangia. Our specimen has veinlets 11–16 to a side, in which single respect it differs from the West Indian plant. The sori become oblong with age, attaining a length of 2 mm.

**Cochlidium Connellii** (Baker) n. comb.

This fern, described as a *Polypodium* from collections of McConnell & Quelch from the summit of Mount Roraima, was re-collected by Mr. Tate at the type locality (no. 448). Its possible relationship with *Cochlidium* (or *Pleurogramme*) is suggested by Goebel (Flora **124:** 24. 1929). Detailed study of the present material and of a fragment of *McConnell & Quelch 570*, cited in Baker's original description (Trans. Linn. Soc. II. **6**:82. 1901) verifies this view. In general appearance and habit and in the position of its sori, *C. Connellii* resembles *C. furcatum* (Hook. & Grev.) C. Chr., a species which Christensen (Dansk Bot. Ark. **6**:17, 20. 1929) has placed here in spite of its polypodioid sori. The present species has coenosori considerably more elongate than those of *C. furcatum*, and its relationship with this group appears certain.

The following notes may be taken as supplementary to the original description:

Rhizome erect, cylindric, slender (1–2 mm. in diameter), densely paleaceous, the scales hidden among the leaf bases, light brown, lanceolate-acuminate from a rounded base, about 3 mm. long, .5 mm. broad near the base, the cells in 10–12 longitudinal series (at the widest point) with thin partition walls; fronds crowded, the stipes short (2–5 mm. long), slender, glabrous, the lamina thick coriaceous, glabrous, linear, 5–9 cm. long, 1.5–2 mm. broad, narrowly attenuate at the base, blunt at the apex, rarely forked near the apex; venation obscure, the costa much-thickened, the veins immersed, alternate, simple, ascending, somewhat distant (about 1 per 1.5 mm. of costa), short (about 2.5 mm. long), the distal part

forming an oblong-linear plate of soriferous tissue (1.5–1.8 mm. long) lying parallel to the costa; coenosori superficial, lying midway between costa and margin on the upper half of the frond, often continguous; sporangia crowded, globose, about .18 mm. in diameter, with two stomium cells, the stalk slender, about .3 mm. long.

**Lycopodium Tatei,** n. sp.

Plant terrestrial, stem short-creeping with upright monostachyous branches; creeping stems dorso-ventrally flattened, 1mm. broad, .5 mm. thick, upper surface nearly plane, lower surface convex; leaves in 8–12 ranks, lanceolate or triangular, those of the lower surface pale and membranaceous, 2–3 mm. long, .5 mm. broad at the base, those of the lateral surfaces subcoriaceous, ascending, 5–8 mm. long,1–1.5 mm. broad at the base, the tip acuminate, rigid, often twisted, the midnerve prominent, leaves of the upper surface fleshy at the base, broadly triangular, 3–4 mm. long, about 2 mm. across the base, tapering to a sharp acuminate point; erect branches cylindric, 4–6 cm. high (exclusive of strobili), 1.2–1.5 mm. in diameter, uniformly leafy, the leaves about 6-ranked, somewhat appressed, lanceolate-acuminate, subcoriaceous, 4–5 mm. long, about .5 mm. broad at the base; strobili 1.5–5 cm. long, about 1 cm. in diameter (including the wide-spreading sporophylls); sporophylls 8-ranked, 5–6 mm. long, 1–1.5 mm. broad near the base (the lower portion triangular, the upper portion lanceolate-acuminate, 3.5 mm. long, .5 mm. broad at its base), subcoriaceous, the midrib strong,the margins minutely serrate,the base truncate to a ligulate attachment .6 mm. long and .4 mm. broad; sporangia reniform, about .8 mm. broad, attached to the inner surface of the sporophyll about .8 mm. above its base (exclusive of the strap-like attachment).

Type, *Tate 350,* collected at Philipp Swamp, Mount Roraima, British Guiana, alt. 5100–5200 ft., 11 Nov. 1927, and deposited in the herbarium of the New York Botanical Garden. It is a species closely allied to and approximating in appearance *L. iuliforme* Underwood & Lloyd, from which it differs by having the creeping stems flattened rather than subcylindric, the sporangia only about half the size, and the sporophylls decidedly narrow (about half as broad across the base as those of *L. iuliforme*). The difference in the shape of the sporophylls is very noticeable and constant; those of the present species appear almost linear, while those of *L. iuliforme* appear broadly triangular.

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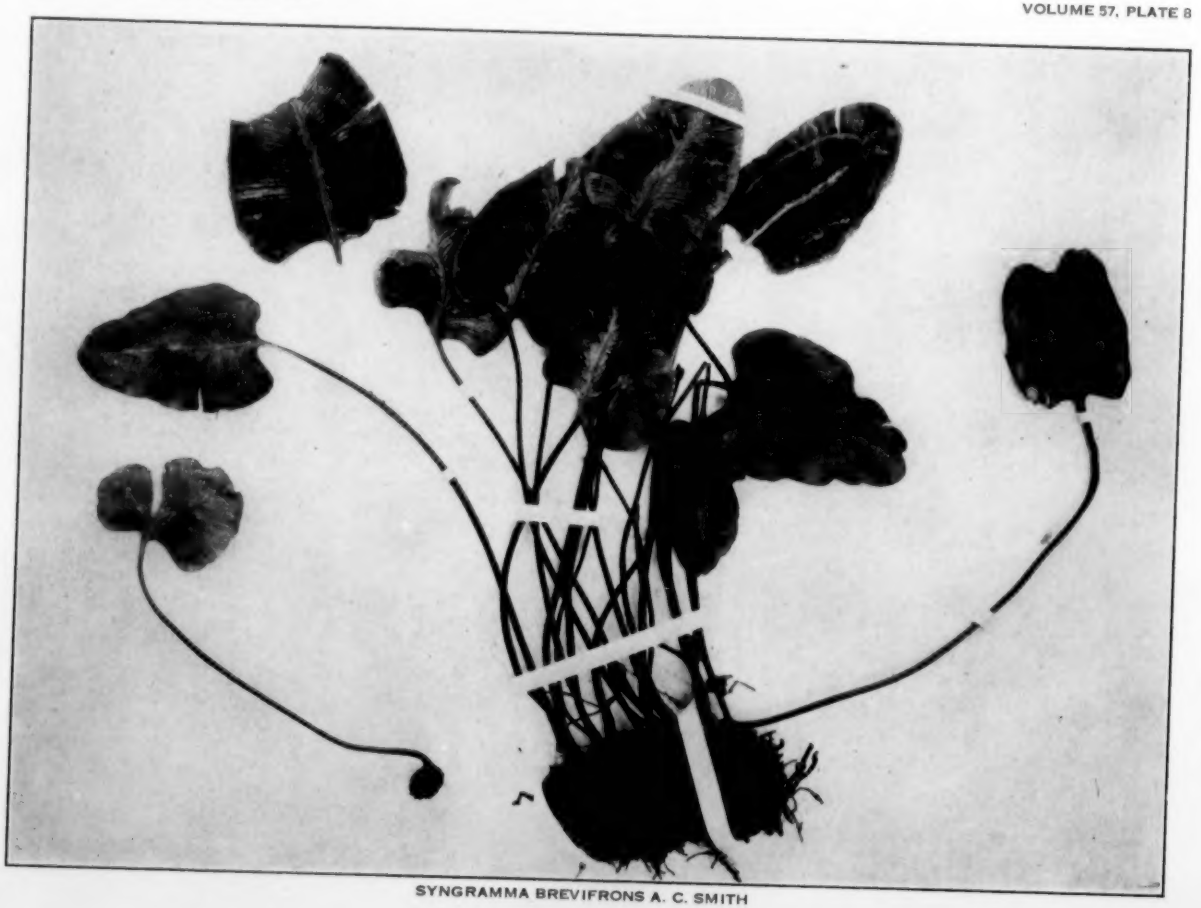
**Explanation of plate 8**

*Syngramma brevifrons* A. C. Smith; photograph of type specimen, *Tate 421,* in the herbarium of the New York Botanical Garden (about 3/4 natural size).



SYNGRAMMA BREVIFRONS A. C. SMITH

UNIV. OF MICH.

## Two new species of Meibomia from Mexico[1]

CONRAD V. MORTON

The following two new species of *Meibomia*, collected by Mrs. Ynes Mexía, were discovered recently while identifying Mexican material of this genus in the United States National Herbarium.

**Meibomia occidentalis** Morton, sp. nov.

Section Heteroloma. Erect shrub, 2–3 meters high; stems terete, sparsely pubescent. Leaves pinnately trifoliate; lower leaves with petioles striate, sparsely pubescent, 11 cm. long, petiolules 5 mm. long, rachis 4 cm. long, lateral and terminal leaflets about equal in size, lanceolate-ovate, evenly and gradually acute at apex, rounded or almost truncate at base, about 12 cm. long, 6 cm. wide, bright green above, pale beneath, glabrous, secondary veins about 10; upper leaves similar but smaller; stipules red-brown (at least in the dried condition), acuminate, cordate and much enlarged at base, the pairs completely encircling the branches, 2.5–3 cm. long on the principal branches, many-nerved, glabrous, persistent even at fruiting time; stipels lanceolate, 1 cm. long or less, glabrous, deciduous in part. Inflorescence of axillary and terminal racemes; rachises puberulent; bracts lanceolate, glabrous, deciduous before anthesis; pedicels usually in pairs, slender, 2–4 mm. long, puberulent; calyx campanulate, 3–4 mm. long, 4- or 5-lobed, the lobes unequal, pubescent; wing petals narrowly oblanceolate, 7 mm. long, keel petals clawed (the claw 1.5 mm. long), 6.5 mm. long, banner 8 mm. long, 3 mm. broad; stamens diadelphous, the odd stamen adnate to the staminal tube for half its length, the tube 7 mm. long; fruiting pedicels 6–8 mm. long; calyx and staminal tube persistent in fruit; loment with 3 or 4 joints, more deeply cut below than above, stalked (the stalk longer than the calyx), not contorted; joints with the upper margin shallowly, the lower deeply rounded, 7 mm. long by 5 mm. wide, reticulate, sparsely puberulent.

Type in the U. S. National Herbarium, no. 1,405,412, collected on the trail to El Ranchito, near San Sebastián, Jalisco, Mexico, alt. 1500 meters, January 11, 1927, by Mrs. Ynes Mexía (no. 1453). A flowering specimen is mounted on sheet no. 1,405,407; it was collected by Mrs. Mexía in Arroyo del Triangulo, San Sebastián, Jalisco, Mexico, alt. 1425 meters, January 1, 1927 (no. 1334).

Mrs. Mexía's field notes state that the plant is an erect shrub with

[1] Published by permission of the Secretary of the Smithsonian Institution.

slender branches, growing in thickets on streamsides and in ravines. The flowers are white inside, purple outside. The buds are red.

Strangely enough *Meibomia occidentalis* is more closely related to *M. bracteosa* of the eastern and southern United States than to any previously known Mexican species. It is amply distinct, however, *M. bracteosa* having a herbaceous habit, smaller and differently shaped stipules, larger flowers, and larger and differently shaped fruit.

**Meibomia saxatilis** Morton, sp. nov.

Section Chalarium. Inclined or erect shrub, 5–7 dm. high; stems terete, glabrous, the branchlets very sparsely pubescent with long, soft, white, appressed hairs. Leaves pinnately trifoliate; petiole 2.5–4 cm. long, angled, very sparsely pubescent with long, soft, appressed hairs; rachis 1–1.5 cm. long; petiolules 4–5 mm. long, thickened, pubescent with more spreading hairs; terminal and lateral leaflets similar in size and shape, elliptic, the largest blades 6×4 cm., dull green, upper surface with a few long, soft, white, spreading hairs (especially on the veins) and with numerous but inconspicuous hairs on the mesophyll (visible only under a dissecting microscope), lower surface glabrous except for the long, white hairs sparingly present on the veins and veinlets, secondary veins 9–11; stipules deciduous, not seen; stipels persistent, subulate-acuminate, pubescent. Inflorescence of axillary and terminal racemes; bracts ovate-acuminate, 5 mm. long, glabrous, ciliate, deciduous at or before anthesis; rachis puberulent; pedicels usually in pairs, 2–4 mm. long, puberulent; calyx campanulate, 4-lobed, the upper lobe 2-toothed, sparsely pubescent, 2–2.5 mm. long; wing petals 8.5 mm. long, keel petals clawed, 8 mm. long, banner 7.5 mm. long, 4 mm. broad, very obtuse at apex; stamens diadelphous, the odd stamen united with the tube for half its length, the tube 7 mm. long; calyx and staminal tube persistent in fruit; loment 2–4-jointed, stalked (the stalk much longer than the calyx, pubescent), equally lobed above and below; joints orbicular, 4 mm. in diameter, sparsely puberulent, the isthmus rather broad.

Type in the U. S. National Herbarium, no. 1,405,414, collected at La Bufa, Real Alto, Jalisco, Mexico, alt. 2500 m., January 30, 1927, by Mrs. Ynes Mexía (no. 1597).

Mrs. Mexía's notes state that the plant grows in crevices of rocks, and that, being eagerly eaten by stock, it is found only on cliffs. The flowers are light lilac.

This beautiful species is related to *Meibomia bella* Blake, which has smaller, more elongate leaves, and much larger flowers in a large terminal panicle.

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## INDEX TO AMERICAN BOTANICAL LITERATURE

### 1927-1930

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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# The phylogeny of maize[1]

G. N. Collins

To retrace the evolutionary path of any existing form is a difficult task. If it were possible to make a really convincing and detailed picture of the phylogeny of maize or of any other species it would constitute a direct proof of evolution and the fundamentalists would be put to rout. Unfortunately the evidence in any particular case is more or less fragmentary and much of it is usually open to more than one interpretation.

Where paleontological records are available they constitute the most direct and convincing evidence. In the absence of fossil remains it is necessary to fall back on the comparative morphology and distribution of related forms. Our problem is to picture how changes in the environment, operating through natural selection, have brought about or preserved modifications. In the case of a domesticated plant the most important environmental factor is man and the trail leads into ethnology or ethnobotany. One point I hope to emphasize is that the widest break in the evolution of most cultivated plants comes at the time when the species is brought into cultivation. For this reason the phylogeny of a cultivated plant centers about the manner of its domestication.

## TAXONOMIC RELATIONS

Our subject, *Zea Mays*, needs no introduction to any one living in the United States. There is, perhaps, no other species of plant known to so large a proportion of the people of the American continent as is maize. The monotypic genus is placed by taxonomists in the tribe Tripsaceae. There are seven genera in this tribe, of which three are American. These are *Zea*, *Euchlaena*, and *Tripsacum*. The tribe Andropogoneae, in which sorghum is placed, is not widely separated from the Tripsaceae. The only important character differentiating these tribes is the existence of perfect-flowered spikelets in the Andropogoneae.

There seems little reason to question the accepted taxonomic arrangement except perhaps to minimize still further the distinction between the

[1] Based on an invitation address presented in a symposium on the Biology of Maize before the joint meeting of Section G (Botany) of the American Association for the Advancement of Science, the Botanical Society of America, the American Phytopathological Society, and the American Society of Plant Physiologists at Des Moines, Iowa, 31 December 1929.

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Tripsaceae and the Andropogoneae. The various forms of maize completely bridge the gap between the two tribes and unless a hybrid origin of maize is accepted it would seem necessary to adopt Hitchcock's suggestion that the Tripsaceae may be no more than a subtribe of the Andropogoneae.

The known forms that need to be taken into account in determining the botanical affinities of *Zea* are few. They are: *Tripsacum*, *Euchlaena perennis*, and *Euchlaena mexicana*. Other genera of the Tripsaceae are not considered. They are Old World forms not closely affiliated with maize. If a linear arrangement is to be adopted the above is undoubtedly the most reasonable sequence.

No detailed description of these plants will be necessary. Doctor Weatherwax (1918) has made a comprehensive study of the comparative morphology of the Tripsaceae and given a clear and detailed picture of the three genera involved.

The series begins with *Tripsacum*, a genus of truly wild plants. The species of *Tripsacum* are poorly defined, with a multitude of intergrading forms and much evidence of hybridization. Taking the genus as a whole it ranges from the north Atlantic states through the Mississippi Valley, Florida, the West Indies, Mexico, Central America, and the northern part of South America. There is also a form in southern Arizona. About eight species have been recognized. Extremes differ profoundly but the existence of intergrading forms makes classification difficult and the number of species uncertain.

Two or three of the species are grown to some extent as forage plants but this practice apparently is of modern origin. The only evidence of use by man in pre-Columbian times is the finding by M. R. Harrington, Museum of the American Indian, of inflorescences of *T. dactyloides* in burial caves in the Ozark mountains. So far as I know the ethnologists have made no suggestion regarding the use by the early Americans of these inflorescences. In this and all other species of *Tripsacum* the seeds are small and embedded in hardened joints of the rachis many times the volume of the seeds. It is scarcely conceivable that the material could be used as food.

All species of *Tripsacum* are perennial. In Mexico the usual habitat is rocky hillsides where the plants are protected from grazing animals. The relationship between *Tripsacum* and *Zea* is remote and the chief reason for introducing *Tripsacum* into a discussion of the phylogeny of maize is that *Tripsacum* is the only American representative of the group of grasses to which *Euchlaena* and *Zea* belong, that is found growing outside of cultivated areas.

The genus *Euchlaena* consists of two species, *E. perennis*, a perennial, and *E. mexicana*, an annual. There are two rather distinct forms of the annual species,—Mexican teosinte that grows as a weed in and about maize fields in a number of localities in Mexico, and Florida teosinte, the form grown for forage in many tropical and subtropical regions of both hemispheres. These two forms of annual *Euchlaena* are easily distinguished and would undoubtedly be accorded specific rank were it not that the characters which differentiate Mexican teosinte from the plant grown in Florida may be due to hybridization with maize. At least crosses between maize and Florida teosinte produce plants that are indistinguishable from Mexican teosinte.

These are the existing wild plants with which maize is most closely associated. The order of their affiliation with maize is not open to question. The first and most closely related form is Mexican *Euchlaena;* second, Florida *Euchlaena;* and third, perennial *Euchlaena*. The next and much more distant relatives are to be found in the genus *Tripsacum*.

## CHROMOSOME STUDIES

In some groups of plants chromosomes studies have furnished valuable evidence regarding phylogeny. This line of attack has not been neglected in *Zea* and its relatives. Both Longley (1924) and Randolph (1928) have made cytological studies of *Zea*, *Euchlaena*, annual and perennial, and *Tripsacum*. Longley has also determined the chromosome number in several members of the sorghum group in the Andropogoneae. The findings are of great interest but their bearing on phylogeny is not obvious.

The normal haploid number of chromosomes in *Zea* is 10. In several stocks of Black Mexican sweet corn, and in at least four other unrelated strains of maize there are many plants with one or two additional chromosomes. It does not appear that these supernumerary chromosomes are duplicates of any in the normal set. No morphological differences or changes in Mendelian ratios have been associated with these extra chromosomes. Although transmitted from generation to generation they produce no visible effect. Except as they provide one more item that distinguishes maize from all its relatives these supernumerary chromosomes seem to have no phylogenetic significance. All forms of annual *Euchlaena* thus far examined also have 10 pairs of chromosomes. In *Euchlaena perennis*, however, there is double this number or 20. Emerson (1929) finds evidence of duplicate chromosomes in *E. perennis*. Our experiments confirm this and it seems fairly safe to assume that *E. perennis* is a tetraploid. This might seem to have some bearing on phylogeny, since it raises the question whether the diploid forms have arisen from the

tetraploid or vice versa. In *Tripsacum dactyloides*, however, where Longley finds 36 as the haploid number, Randolph found plants from Kansas having but 18 pairs. When grown side by side the 18 and 36 chromosome forms are distinguishable but the differences are slight and of a quantitative nature. It would seem, therefore, that in this group of plants the doubling or halving of the number of chromosomes is of little importance except in providing some measure of isolation by reducing the interfertility of the two forms. Three other species of *Tripsacum* examined by Longley all had about 36 pairs of chromosomes.

The work with chromosomes has brought to light a rather striking parallel between *Euchlaena* and the sorghums. In both groups forms with double the basic number are perennial, producing rhizomes, while all forms with the basic number are annual. It may, of course, be a coincidence that the only 2n forms that have been found thus far are two perennial species of sorghum and *Euchlaena perennis*.

In this group of plants there is no clear indication that evolution or increased specialization is accompanied by a change in the number of the chromosomes. In *Zea* we know that specialization and simplification are to a large extent the result of the segregation of individual genes unassociated with any change in chromosome number, and for this reason *Zea* should perhaps be left out of the picture.

The annual habit is usually thought to have been derived from the perennial and this change is here associated with a reduction in chromosome numbers. *Euchlaena* is more highly specialized than *Tripsacum* and again the more highly specialized form has the smaller number of chromosomes. In the latter comparison, however, the basic number is different in the two forms and the relationship is probably of a nature entirely different from that existing between the annual and perennial forms of *Euchlaena* and sorghum.

## WHERE WAS MAIZE DOMESTICATED?

The geographical region where maize was domesticated was one question about which there seemed no room for controversy. *Euchlaena*, the wild plant most closely related to maize, is known only from Mexico. This evidence was considered conclusive and argument was confined to the rival claims of particular Mexican localities.

Vavilov has now come forward with the theory that the center of distribution of any cultivated species is the region showing the greatest number of distinct types. If this criterion be applied to maize the center of distribution would be northwestern South America and not Mexico, for the region that includes Peru, Bolivia, and Ecuador can

show a greater diversity of maize types than the whole North American continent.

If *Euchlaena* be denied any part in the domestication of maize the argument for Mexico as the place of origin is very much weakened. There is also the fact that the fossil ear of maize came to light in Peru although the place from which it came originally is not known.

The diversity of maize types in South America is closely associated with the diversity of soil and climate and with the large number of isolated situations. It seems certain that these conditions would provide a wealth of diversity in the native vegetation and would afford more abundant materials for domestication than any less diversified region. Cook (1925) has pointed out that no other region equals Peru as a center of domestication. If, however, *Euchlaena* did play a part in the origin of maize and from Mexico it spread to South America after its domestication, the isolation into localities with different environments would result in diversification and the present situation would be brought about.

## DOMESTICATION THE CRITICAL POINT IN PHYLOGENY

Everyone will admit that all the plants in question have descended from a common ancestor if we go back far enough for the ancestor. Weatherwax (1918) has given a description of a theoretical ancestor and states that 'from this plant the three genera here considered, and probably the other genera of the Maydeae (Tripsaceae) and some of the Andropogoneae as well, have been evolved by the suppression of parts, whose rudiments are, in most instances, still to be found in the modern plants.' The work of Weatherwax provides a very satisfactory picture of the differentiations of these natural groups, including some form possessing many of the characters of *Zea*.

In attempting to picture the origin of maize itself, however, we may be practically certain that natural evolution is not the final agency. At some point in the ancestry of maize man took charge and natural selection was replaced by artificial selection.

We can scarcely credit primitive man with sufficient foresight and altruism to preserve plants useless to himself for the benefit of posterity. As an incentive to selection there must have been some plant that was useful to him in the wild state.

The nature of this plant which man began to protect seems to me the crux of the problem. We are in a situation somewhat similar to that confronting Darwin when he sought to retrace the operation of natural selection to the point where small variations of no survival value were the only available material for selection.

The characters in which maize differs from existing forms and for which an explanation is sought are largely of a nature that makes maize more useful to man but less adapted to survive in nature. Very briefly the more important of these characters are the rigid and enlarged rachis of the pistillate inflorescence, the naked seeds, the bracts enveloping the ear, the paired pistillate spikelets, and the intolerance to self fertilization.

## THEORIES OF DOMESTICATION

To bridge the gap between the wild ancestors of maize and the cultivated plant a number of hypotheses have been suggested. It may as well be admitted at once that no hypothesis has yet been advanced that does not disregard facts or strain credulity. It is clearly a subject regarding which any conclusion must be tentative. The several hypotheses that have gained currency will be discussed briefly and some of the objections to each will be indicated.

## MAIZE A NATURAL SPECIES

The first theory to be considered is that maize in practically its present form at one time existed as a wild plant.

The chief evidence in support of this hypothesis is historical rather than botanical, and the credit for its discovery belongs to Mrs. Zelia Nuttall (1927, 1930), the distinguished ethnologist who has discovered in the writings of Boturini (1746) a direct statement that maize was growing wild in the hot lands of Mexico between 1735 and 1743. Mrs. Nuttall's translation of Boturini's statement is as follows:

> I found, in New Spain, a wild maize that grows in the forest or woods, especially in those of the hot lands, with a small ear whose few grains are of a more delicate flavour than the cultivated kinds, as though nature had located in them, as in a compendium, all of its essence.

To an ethnologist it is natural that this direct statement should appear conclusive, but botanists familiar with the lack of natural adaptation in maize will surely consider the possibility of Boturini's having been mistaken. Was the plant to which he refers really growing wild? Or was the plant really maize? The objection to this simple explanation is the complete disappearance of wild maize and the improbability that any plant able to survive in competition with native vegetation could be sufficiently like the plant as we know it to be called maize.

In connection with Boturini's statement the reference to wild pod corn in Paraguay should be mentioned. The origin of this claim has been discussed elsewhere (Collins, 1923) and dismissed as very improbable. Although somewhat better adapted to survive under natural conditions

than ordinary maize, no known form of pod corn would be likely to persist without man's protection.

I wish again to urge the importance of additional information regarding a type of maize with a branched terminal inflorescence and naked seeds that is mentioned by Azara (1809) as occurring in Paraguay.

## ORIGIN BY GROSS MUTATION

We may next consider the possibility of maize having arisen as a mutation or sport in some wild species.

The difficulties in picturing the transition from a useless wild grass to maize may be swept aside if we can bring ourselves to have sufficient confidence in the possibilities of mutation.

Abrupt changes in the germ plasm accompanied by profound and simultaneous morphological changes in many of the organs are not unknown in maize. So far as morphological differences are concerned some of these mutations such as andromonoecious dwarf and ramose maize represent changes of the same order of magnitude as would be required to transmute some wild plant into maize. We know that most of these mutations behave in inheritance as simple Mendelian characters and it is not unreasonable to assume that they arose suddenly as gene mutations without the existence of intermediate stages.

The most serious objection to the mutation hypothesis is the complete series of intermediate forms that are produced when maize is crossed with *Euchlaena*. When gene mutations are crossed with the parent stock from which they arose the first generation may or may not exhibit the new form but in the second generation there is segregation into the two parental types. This is the observed behavior of all gene mutations of maize. In fact a behavior of this type is the reason for diagnosing the case as a gene mutation. If the gene mutation is the culminating change in a series that produced no visible effect until completion, the ratio of mutant forms to normal forms is reduced as the number of factors is increased. If the number of factors involved is sufficiently large a recessive mutation might not reappear at all after crossing with the normal stock. The failure to recover some apparent mutations is probably to be explained in this way. But in any case no series of intermediate forms is produced. I can recall no mutation or heritable sport that does not behave more or less as a unit when crossed with the stock from which it sprang.

Crosses between *Zea* and *Euchlaena*, which is the best representative of the stock from which maize may be assumed to have mutated, do not behave as gene mutations. On the contrary the result is a series of inter-

mediate forms more nearly resembling a back cross between a hybrid of diverse ancestry and one of the parental lines.

It is, of course, unnecessary to assume that the parental stock from which maize may have mutated was *Euchlaena* as we now know it, but the similarity in chromosome behavior of *Zea* and *Euchlaena*, taken with the fertlity of the generic hybrid, indicates rather definitely that the differences between the two forms are gene differences and that any common parental stock must be assumed to have a similar chromosome complex. The multiplicity of gene difference between *Zea* and *Euchlaena* seems to me a serious objection to the 'origin by gross mutation' hypothesis.

It might be urged that the mutation was of another kind, involving a simultaneous change in a large number of genes. There is no parallel of this type of mutation in maize or anywhere else so far as I know, and to explain the origin of maize in this way is, practically speaking, to fall back upon special creation.

Origin by mutation makes no demand on time and should be popular with the ethnologists, but Blaringhem (1907) is the only botanist seriously to advance the theory. Blaringhem claims to have induced heritable mutation by injuring the plants and believes that maize arose from *Euchlaena* by this means.

### MAIZE DERIVED FROM EUCHLAENA

Harshberger's (1896) hypothesis that maize arose from *Euchlaena* or some closely related plant by human selection and recrossing with *Euchlaena* will next be considered.

Maize and *Euchlaena* are closely related plants and this theory may seem a reasonable explanation, in that it derives the cultivated species from the nearest existing wild form.

This theory assumes that *Euchlaena* was a cultivated plant and there is no reliable evidence that *Euchlaena* is or ever was of use to man except as a forage plant for domestic animals, and the early Mexicans had no domesticated herbivorous animals.

The only evidence suggesting the use of *Euchlaena* that I have been able to find is: (1) the statement by Hernandez (1790, p. 122), referring to *Euchlaena* which he calls 'cencocopi,' that 'the seeds, ground and eaten to the weight of an ounce, cure dysentery.' It should be noted in this connection that the plant called 'teosinte' by Hernandez is not *Euchlaena*, but some entirely different plant, probably a cycad. (2) The statement contained in Rossignon's (1869, p. 187) letter transmitting seeds of teosinte to France, which is to the effect that 'the inhabitants of Santa Rosa in Guatemala eat the young shoots and use the leaves and stalks.' Here

again it is very doubtful if the plant referred to is *Euchlaena*. *Euchlaena* has never been collected in Guatemala and the name 'teosinte,' under which the seed was submitted, is not now applied to *Euchlaena* in Guatemala.

Any plant with the characters of *Euchlaena* would be most unpromising material from which to develop a food plant. As a starting point for selection in the direct line it would seem that we must go back to a plant that had not developed the indurated rachis that encloses the small seeds in both *Euchlaena* and *Tripsacum*.

In crosses between *Zea* and *Euchlaena* the second generation gives a series of completely intergrading forms. Do these intermediate forms represent stages in the evolution of maize? Apparently they do not. Evolutionary stages in the phylogeny of any form must have had survival value, and it appears that the intermediate stages that result from this cross are not able to persist under natural conditions nor are they preserved by man.

## INDEPENDENT EVOLUTION OF MAIZE

We next come to the hypothesis advanced by Weatherwax (1918) that maize is the culmination of an independent ancestral line that originated at or before the time when the ancestors of *Euchlaena* and *Tripsacum* became differentiated. This theory accommodates the facts indicating that maize occupies a position intermediate between the other members of the Tripsaceae and the Andropogoneae and by substituting an unknown wild ancestor it becomes unnecessary to assume that *Euchlaena* was of use to primitive man.

This most natural and direct explanation does not appeal to the ethnologists because of the demand for time. The change brought about by man's selection during the past 1000 years is extremely slight compared with the change that must have taken place since the ancestors of maize became an object of man's protection. Excluding gross mutations and assuming anything like a uniform rate of change 20,000 years would seem well below the time requirement.

Since man appears to be the most influential factor in the evolution of maize we naturally seek all possible information regarding the length of time that he has been operating and the region or regions where he practised his art.

The American origin of maize is unquestioned, hence the domestication of maize must have taken place since the advent of man on the American continent. Anthropologists seem a bit niggardly in allotting time to man in America. Not only was the work accomplished, but all traces of where

or how the task was done have disappeared so completely that the origin of maize, at least, can be presented only as a series of suggestions and inconclusive hypotheses.

It should be kept in mind that only a part of the time allotted to man in America can be utilized for the work of domestication. We know that the domestication of maize was completed some thousands of years ago. Dated monuments carry man's life in America back to about the time of Christ. Ears left by the basketmakers and those in the prehistoric caves of South America attest the fact that maize was completely domesticated at a still earlier date, while the fossil ear of maize found in Peru was said by Knowlton (1919) to be at least several thousand years old and it was out of deference to the ethnologists that Doctor Knowlton did not suggest a still earlier date.

Fortunately a few buried spearheads promise to open the hearts of the ethnologists where botanical evidence has been of no avail and the time requirements of the theory of independent evolution need be no serious obstacle to its acceptance.

The principal shortcoming of the theory that maize developed independently of *Euchlaena* is its failure to take into account the close relationship of *Zea* and *Euchlaena* indicated by their interfertility.

A great many types of maize have been crossed with *Euchlaena* and it appears that there is complete interfertility between all the types of maize and both forms of annual *Euchlaena*. Reciprocal crosses between maize and perennial *Euchlaena* also are made without difficulty and the crosses are fertile. The environmental requirements for this hybrid are, however, somewhat exacting, and the fertility is not complete.

In crossing *Euchlaena perennis* and maize the cross is between forms with 20 and 10 chromosomes respectively, and sterility, at least in the pollen of the $F_1$ plants, seems to be associated with the irregular distribution of the chromosomes.

In a single cross between perennial and annual *Euchlaena* irregularities in the formation of pollen are of the same order as in hybrids between maize and perennial *Euchlaena*. That the perennial and the annual species of *Euchlaena* are phylogenetically very close to one another will scarcely be questioned and it seems reasonable that a similar difference in chromosome number between maize and perennial *Euchlaena* should result in a corresponding reduction in fertility.

Maize and *Euchlaena* are hosts to the same parasitic diseases. There is close agreement between the two forms in the number, shape, size, and behavior of the chromosomes. These facts and the complete interfertility

of maize and annual *Euchlaena* make it difficult to believe that these two forms have remained distinct since the origin of the Tripsaceae.

## HYBRID ORIGIN

The theory of hybrid origin proposed by Harshberger (1896) and later amplified by the speaker (Collins, 1912) is in agreement with that of Weatherwax, except for the assumption that the hypothetical phylogenetic line coordinate with those of *Tripsacum* and *Euchlaena* at some time became hybridized with *Euchlaena*.

We may admit the common ancestor of *Tripsacum*, *Euchlaena*, and *Zea* without assuming that these lines have remained distinct since their original divergence. If it be held that the ancestral lines of *Euchlaena* and *Zea* have remained separate since they originally diverged from some perfect-flowered form, the complete interfertility of annual teosinte and maize constitutes a unique example of fertility between distantly related forms. The ease with which *Euchlaena* and *Zea* may be crossed, the perfect fertility of the hybrid, and the regularity of segregation bespeak a closer relationship.

*Euchlaena* behaves like a normal wild species. There is great adaptability to change in environment but little in the way of genetic segregation or change. Mutations are practically unknown. *Zea*, on the contrary, shows less environmental adaptability but is constantly segregating. Mutations are frequent and the production of monstrous abnormalities is of common occurrence. Its germ plasm normally contains a very large number of genes in a heterozygous state. It is not even very definite regarding the number of its chromosomes.

Such a condition does not prove that it must be of hybrid origin but the facts must be taken into account if a plausible picture of the ancestry of maize is to be presented. It should be obvious also that the phylogeny of maize may not be considered apart from its domestication. This is more particularly the case with maize than with most of our domesticated plants, for maize is more dependent on man for its existence than is any other of our cereals.

As with all other suggested explanations there are serious objections to the theory of hybrid origin. The old objection that hybrids between species are of rare occurrence has to a large extent been disposed of by recent work in the borderland between taxonomy and genetics. Fertile hybrids between natural species are now accepted. These would doubtless be much more common were it not for the geographic isolation that so generally separates species. If one of the species is a cultivated plant the

migrations of man remove the obstacle of geographic isolation and greatly increases the opportunities for hybridization.

The difficulty is not the improbability of the occurrence of interspecific or intergeneric hybrids, but that up to the present time it has not been possible to hybridize maize or *Euchlaena* with any member of the Andropogoneae. Another disturbing fact is that among the multitude of observed mutations of maize few pronounced *Euchlaena*-like characters have appeared.

This confusing array of conflicting hypotheses is a poor substitute for the picture of the evolutionary history of maize promised by our title. However we may derive consolation from the thought that a final and convincing solution might be less conducive to further research than is the present unsettled condition.

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# The ontogeny of the maize plant[1]

PAUL WEATHERWAX

The logical place to begin an account of the ontogeny of a plant having a sexual origin is at the very beginning of its individual existence, that is, at the time of fertilization. In the case of the seed plants, however, we may select a more tangible and more stable starting point, and in outlining the life history of the maize plant we choose to begin with the seed.

In maize, as in most other grasses, the seed is closely invested by the pericarp which largely takes the place of the testa. The seed proper consists of a well-developed embryo, a large endosperm, and the vestigial testa.

As germination takes place a definite series of changes occur in the embryo, and many parts of the seedling show little resemblance to their forerunners in the embryo. The primary and lateral roots, already well formed before the maturity of the seed, elongate and make contact with a water supply; the mesocotyl elongates, bringing the plumule to the surface of the soil (if the seed has been planted underground); and the plumule bursts its sheath and its leaves unfold and are soon ready for photosynthesis.

In the meantime the cotyledon has nourished the developing axis of the seedling by making available the food stored in itself and by digesting and absorbing the endosperm. Such a generous supply of the latter is present, however, that the seedling is usually self-supporting long before its reserve is exhausted.

The mesocotyl, that portion of the axis of the embryo between the base of the coleoptile and the place of attachment of the scutellum, is a structure of great interest in many ways. About the interpretation of it are centered the various theories as to the morphology of the embryo. These theories fall into two main groups with various modifications. One view holds that the scutellum, the coleoptile, and the outer portion of the mesocotyl, taken together, constitute the first leaf of the plant. The other view maintains that the scutellum is the cotyledon, it being the first, and the coleoptile the third leaf of the young plant. The second leaf, represented by the epiblast in some grasses, is absent in maize.

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Regardless of its morphological nature the mesocotyl plays an important part in germination. Its elongation brings the plumule to the light and air, and the depth to which a seed may be planted with promise of successful germination depends upon the ability of the mesocotyl to elongate. Some varieties grown by the Indians of the dry regions of the southwestern part of the United States have this ability so developed that the grains may be planted as much as 18 inches deep.

The parts of the seedling below the base of the coleoptile, as well as the first few leaves above this point, play a very important part during germination, but their inability to continue development limits them to only a temporary importance. Neither the roots nor the mesocotyl have any method of continued increase in diameter, and the first leaves arrive at maturity on a scale of development too low to permit a long-continued functional activity. The entire portion of the plant,—leaves, stem, and roots,—which is active during the periods of rapid growth and maturity, is derived from the plumule.

As growth carries the terminal bud forward the stem is formed as a series of segments arranged end to end and separated by nodes. A single leaf arising from the upper end of each internode subtends a bud, or the primordium of one, which is borne in the embryonic region of the lower end of the internode next above it. A whorl of roots is also produced from this same embryonic region in the lower parts of the stem. Each segment of the developing plant thus resembles a miniature plant in itself, having its stem, its leaf, its roots, and a basal bud. The stem portion of each of these phytomers is formed by the progress of the growing point and a limited amount of subsequent cell division. Elongation and maturation soon bring cell division to an end, and, in the absence of any cambium-like tissue which might continue the production of new cells, a limit is soon reached in the growth of the internode in diameter.

The dimensions of each internode may thus be regarded as a quantitative expression of a set of physiological conditions present at the time of its formation. When the plant is young and its root system and leaf area are small, it forms internodes of small diameter. Successive segments of the stem have a larger and larger diameter, correlated with better nourishment, until a maximum is reached. Subsequent to the attainment of this maximum there is a gradual decrease in diameter due to the diversion of energy into axillary buds, or to accelerated growth in length, or both.

Elementary treatises on stem growth often state that stems which have no cambium increase in diameter by multiplication and differentiation of the parenchyma. This statement, following a discussion of growth

in diameter in stems having a cambium, is misleading, because in such cases as the one at hand it may be interpreted as implying that the small internodes first formed in the germination of a grain of corn grow until they are an inch or more in diameter. Such is not the case. As a corn plant develops it acquires internodes of a larger diameter, not by expanding small ones, but by building new ones on a larger scale.

A few nodes above the ground there is usually a cessation of the development of roots on the stem, and above the uppermost fully developed ear the axillary buds are usually no more than meristematic rudiments.

The total number of nodes and internodes that the vegetative stem of the plant is to have will have been formed, and the terminal inflorescence will be developing, by the time the plant is a few weeks old, the exact time depending much upon the variety, the weather conditions,and probably the relative length of day and night. At this time the actual length of the stem itself is only a small fraction of the height of the plant, for the long leaf sheaths conceal the end of the stem and hold the crown of leaf blades high above it.

A rapid elongation of all the internodes, except a few of the lowest, now begins; after a time the terminal inflorescence emerges from the uppermost leaf sheaths; and ultimately many or all of the nodes are exposed above the tops of the sheaths. This elongation results from growth in the meristematic region at the lower end of each internode, the more mature part of each internode being at its upper end.

This method of growth in length leaves for a long time at the lower end of each internode a weak place which would have disastrous consequences if it were not for the support afforded by the firm leaf sheath which is rigidly attached at the upper end of the next lower internode. In old stems this embryonic tissue is greatly reduced in extent by maturation, but a small portion probably remains until the plant is at least past flowering, as is shown by its success in orienting itself by geniculate bends at the nodes after being blown over by the wind.

It may be suggested here that in breeding corn for resistance to damage by wind it may be well to consider the quality of the leaf sheath quite as much as the stiffness of the matured portion of the culm or the nature of the root system.

In the course of the development here outlined the inflorescences have been formed. Of these the one terminating the main stem is usually staminate and those on aerial axillary branches are usually pistillate. Those terminating basal suckers show all gradations between the other two types. This sexual differentiation in the inflorescence is due to a differential suppression of flower parts. At its first appearance in ontogeny

every flower of maize has the primordia of three stamens and a pistil. The suppression of the stamens or of the pistil results in a pistillate or a staminate flower, respectively.

We have at present no adequate explanation of the uniformity with which one sex or the other is suppressed in whole inflorescences, but the two types of inflorescence are at sufficient distance from each other on the plant, and there is sufficient lapse of time between the formation of the terminal and the lateral units, to support the assumption that there is some significant physiological difference between them. Careful determinations of hydrogen ion concentration, metabolic rate, or carbohydrate-protein ratios might point out the mechanism of this differentiation.

On the development of the inflorescence little thorough work has been done in recent years. A new study of the regions of growth and method of branching in the young inflorescence would give significant information. Both the male and the female inflorescences show a great range of variation, and only the forms which ordinarily occur can be treated here.

In the fully developed staminate inflorescence the spikelets are arranged in pairs in an open panicle. The branches of this panicle show a definite dorsiventrality, the pairs of spikelets being arranged in two rows on each rachis. On the terminal portion of the central axis of the panicle, however, the pairs of spikelets are arranged in several rows. In both the central axis and the branches the oldest spikelets are near the tips and the youngest at the bases. In a large panicle several days may elapse between the first and the last flowering.

The structure and development of the axillary pistillate shoots is similar to that of the main stem. Here, however, the internodes elongate much less and the blades of the leaves are variously reduced or almost entirely lacking. The sheaths, which are wide and firm, constitute the husks of the ear. When more than one axillary shoot is present the upper is usually the largest and best developed, those below showing a structural and functional reduction correlated with their respective distances from the uppermost functional shoot. When two or more ears are developed on the plant they are at adjacent nodes of the main stem. Branches of the second order may develop in the axils of the husks of the pistillate shoot; these have the same structure as the parent shoot, and, under some conditions, the same ability to develop functional inflorescences.

The pistillate spikelets are borne in pairs on very short branches which are ordinarily arranged in four or more longitudinal rows on the main axis. This arrangement ultimately produces an ear with eight or more rows of grains. The first flowers to mature are neither at the base nor at the tip but somewhere between, usually nearer the base.

The staminate and pistillate spikelets, though very different in appearance and function at the time of flowering, have the same structural plan throughout and are identical in appearance in early stages of development. Each has two glumes, two lemmas, two paleas, and two flowers. The rachilla is very short and there is no visible evidence that it is prolonged beyond the upper floret. Of the two flowers the upper is the more advanced in development, a condition exactly the reverse of that found in the species of grasses which have more than two flowers in the spikelet.

In the spikelets of what is eventually to be the male inflorescence all the parts of each flower develop uniformly to a certain place where suppression of the pistils begins. This is usually very early,—before the ovary wall is complete and while the ovule is still only a meristematic protuberance. The stamens and lodicules continue development, and the mature spikelet has two staminate flowers.

Meanwhile one of the staminate spikelets of each pair has developed a pedicel, but the other usually remains sessile. The usual order of flowering of the four flowers of a pair of spikelets is: the upper flower of the upper spikelet, the upper flower of the lower spikelet, and then the two lower flowers in the same order. Modifications of this order are due to variations in the relative ages of the two spikelets and apparently never to a reversal of the order of maturity of the two flowers of any one spikelet.

The development of the pollen grain shows no striking deviations from what might be expected. The ordinary number of chromosomes is 20 ($2\times10$), but other numbers are encountered; these, like certain variations in the size, shape, or behavior of the chromosomes, are correlated with vegetative peculiarities. The mature pollen grain is spherical or slightly tetrahedral; it has a single germ pore. The antheridial cell divides, producing the two small, crescent-shaped sperms, before the pollen grain is released.

When the time of flowering arrives the lodicules quickly expand, separating the lemma and palea, the filaments elongate, carrying the anthers well out of the bracts, each loculus of the anther opens by a pore at its distal end, and the pollen falls out, usually within a few minutes. Gravity and air currents are the only agents of pollen distribution, and the large amount of pollen produced is correlated with the inefficiency of this method of dispersal.

In the spikelets which are to become pistillate the story is much the same up to the time of the differentiation of the pollen mother cells in the anthers of the upper flowers. At this point there is initiated an extensive suppression of parts, affecting the entire lower flower and the stamens and lodicules of the upper, so that at anthesis the spikelet has left in functional form only a single pistillate flower.

The pedicels of the pistillate spikelets are so short that they are usually ignored and the spikelets regarded as sessile. These short pedicels are attached to a peduncle which is in turn attached to the main axis, the cob. This peduncle is so short that it is also usually overlooked, but sufficiently real so that pairs of grains firmly attached to it can be removed from the mature ear.

A noteworthy variation from the course of development described above is seen in some rather stable varieties of sweet corn. Here only the stamens and the lodicules of the lower flower are suppressed and the spikelet comes to anthesis with two fully developed pistillate flowers and ultimately produces two grains. The resulting crowding causes a rearrangement of grains and often obliterates all trace of the straight rows seen on an ordinary ear. Other irregularities in the rows of grains are due to the occasional occurrence of the pistillate spikelets in threes instead of pairs, or to the failure of a row of pairs of spikelets to extend the full length of the ear.

There is good evidence to support the theory that the pistil is composed of at least three, and possibly six, carpels; but this evidence is anatomical rather than ontogenetic.

The wall of the ovary originates as an asymmetric, collar-like structure around the central protuberance which is to become the single ovule. When this wall has completely enclosed the ovule a protuberance at its top continues to develop into the long style, commonly known as the silk. This structure frequently develops to the length of a foot or more before its tip is exposed beyond the ends of the husks. It bears numerous stigmatic hairs at its cleft tip and throughout most of its length.

Two integuments are formed around the base of the young ovule. The inner of these grows until it entirely surrounds the nucellus except for the micropyle, but the other does not develop that far. In the meantime the ovule has turned partly into the anatropous position.

There are no unusual features in the early stages of development of the embryo sac. Only the chalazal member of the linear tetrad of megaspores survives, and it produces the ordinary seven-celled embryo sac. The polar nuclei come together and remain in contact, without uniting, until the time of fecundation. The original three antipodal cells begin division shortly after their formation and finally produce a considerable mass of tissue,—sometimes as many as 50 to 100 cells,—before their progress is arrested by other developments. In this condition the embryo sac awaits the arrival of the pollen tube.

The pollen grain usually begins germination within less than an hour after falling on the stigma. The pollen tube enters the style by way of

one of the stigmatic hairs and rapidly grows downward through one of the strands of special conducting tissue accompanying each of the two vascular bundles. Although it has a long way to go to reach the ovule, it grows with such rapidity that fecundation frequently occurs less than 24 hours after pollination. Soon after the growth of the pollen tube through the style the latter loses a part of its moisture and ceases to develop. If, however, pollination be prevented, the style will continue to grow for several days.

Many pollen grains may germinate on one style, if they happen to arrive at near the same time, and numerous tubes of different lengths may start on their way toward the ovary, but presumably one of them finally far surpasses all the others. There is often a marked difference in the rate of growth of pollen tubes, when several are growing in the same style. This is thought to be due to genetic differences, and it may give the effect of selective fertilization.

The exact course of the pollen tube after it reaches the ovary has not been determined, but in time its distal end arrives at the micropyle, makes its way through into the embryo sac, and empties its contents. Of the latter we are further concerned with only the two sperms. It is generally admitted without proof that one sperm unites with the egg, and, since the discovery of double fecundation and the contemporary experimental studies on xenia, it has been suspected that the nucleus of the second sperm unites with the two polar nuclei to form the endosperm nucleus. These theories have been confirmed by at least three cytological studies, and there seems now no reasonable doubt that the endosperm receives a part of its heritage from the male parent of the embryo.

The embryo develops much as in related plants. Early cell divisions and growth produce an elongated, pear-shaped structure, the narrow basal part of which becomes the suspensor, while the hemispherical upper portion develops into the embryo proper. As the latter elongates,the cotyledon appears as a lateral lobe growing upward and toward the central part of the ovule. The plumule is formed at the upper end of the axis. Its leaves arise as a series of crescent-shaped invaginations of the growing point. Usually as many as four or five leaves are formed before the seed is mature, and some of these subtend buds. The development of the coleoptile has not been worked out in full detail, but it differs from the other leaves of the plumule (if it is a leaf) in having the form of a closed cylinder, while the others are open along one side. The primary and secondary roots are differentiated in the solid tissue of the lower part of the embryo proper and finally split out of the surrounding coleorhiza. The root cap is the last portion of the root to be split off the sheath, and

its tissue resembles that of the sheath much more than that of the root proper.

The antipodal tissue, which is morphologically the equivalent of the endosperm of typical angiosperms, usually ceases development soon after fecundation and is finally absorbed by the developing endosperm. In some instances, however, it persists and forms a small part of the endosperm of the mature seed.

In early stages of development the endosperm shows a much greater vigor than the embryo. The nucleus resulting from the triple fusion divides, and its descendants divide again and again, producing a large number of free nuclei which distribute themselves around the periphery of the endosperm cell. Later the formation of cell walls begins at the outside and proceeds toward the center, finally resulting in a homogeneous cellular tissue. Growth in the endosperm is accomplished chiefly by a meristematic layer of cells near the periphery, and the central portion soon matures as a somewhat specialized parenchyma. As the time for the maturity of the seed approaches, the outermost layer of cells of the endosperm become differentiated from the rest in that they are filled with aleurone grains and contain no starch. At the base of the endosperm, near the place where the vascular supply enters the ovule, there is another differentiated region which doubtless serves a placental function. In early stages of development the endosperm almost completely surrounds the embryo, but the rapid asymmetric development of the former soon leaves the latter imbedded in its side. A recent study has shown that the apparently exposed side of the embryo is, however, really covered by a thin layer of endosperm when the grain is mature.

As the seed develops and matures, the endosperm destroys the nucellus, and the embryo destroys a part of the endosperm. In each case the tissue destroyed is composed of old, vacuolate cells which apparently contain little food except that which is in solution. This fact favors the theory that most of the food absorbed by the endosperm enters by way of the basal placental tissue. It also indicates that the food absorbed by the scutellum is transported for some distance through the endosperm. Both of these activities indicate a rudimentary vascular specialization in the middle of the endosperm. This is further shown, too, by the fact that, although the endosperm is nourished from the base, the deposition of starch begins at the top and proceeds downward. The ultimate physical texture of the endosperm is determined in part by hereditary patterns of distribution and in part by the extent of starch deposition. A floury endosperm is essentially one that might have been flinty if hereditary or environmental limitations had not prematurely stopped its development.

The development of pigment is one of the last steps taken in the maturation of the endosperm. The aleurone layer may be white, red, blue, or light brown, and mosaics of reds, blues, and whites are common. The more deep-seated parts may be yellow or white. These colors are not to be confused with the series of reds and browns occurring in the pericarp.

The endosperm of such plants as this was originally regarded as only a nurse tissue having no individuality and no significance except as a means of nourishing the embryo. The nuclear fusion that initiates its development, however, and the manner in which hereditary characters may be expressed in it, suggest that its origin is sexual; and the relatively high degree of specialization of its tissues further indicates its individual nature. As an individual, however, it is unique, for it regularly has three ancestors and never leaves any descendants.

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# The genetics of maize[1]

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(with one text figure)

In a general botanical symposium such as this, it would seem that the broader and more recent aspects of this genetical subject should be of greater interest than the detailed, technical developments. The layman often becomes weary of the expert who delights in telling him 'more and more about less and less.' Moreover, the time limit definitely precludes any very detailed presentation. Accordingly, I shall attempt a general picture of what has happened during the past decade in the field of maize genetics.

Maize has now been sufficiently analyzed genetically and cytologically to make it reasonably certain that its chromosomal mechanism of heredity is of the orthodox or *Drosophila*-like type. The ten pairs of corn chromosomes undergo typical parasynaptic conjugation and assort at random. There are no major deviations from what might be called normal, neo-Mendelian inheritance. With the possible exception of a few 8-rowed varieties like the Black Mexican and Golden Bantam sweet corn, as well as some flint varieties, which possess more than 20 (21 to 28) chromosomes, maize is relatively free from abnormal cytology.

Both the independent and linked types of inheritance prevail; and crossing-over occurs in micro- and megasporogenesis with almost equal frequency, albeit with some small variability. On the whole the genetic mechanism has proven remarkably stable; and has enabled maize geneticists to exchange material with assurance that they may still remain on speaking terms with their colleagues.

The general botanist is perhaps interested in knowing the types of hereditary characters and the parts of the plant they affect, which have been discovered up to date. For this purpose I have prepared a chart in which are outlined the known hereditary characters of maize, showing the number of genes concerned in their development (table 1).

First, we may direct attention to the hereditary characters that involve the entire plant. The most striking of these is that called Teopod

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(from *teo*-sinte and *pod*-corn), since it affects the whole plant, leaves, stalk, and inflorescence, producing what is to all appearances another species of *Zea*. This hereditary complex, surprisingly enough, is due to but a single, dominant gene. Teopod is completely fertile with maize and segregates in a typical monohybrid manner. Its chromosome mechanism is apparently normal. Teopod is a convincing example that Mendelian genes govern far more than superficial or varietal characters.

General plant height is determined by two sets of genes, one, a series of quantitative factors; the other, a more precise set of qualitative genes. The latter are investigated through their recessive effects which give us the series of dwarfing genes, eight in number, up to date.

Suckering in maize is unquestionably hereditary, but the details of its genetical make-up have not yet been reported. Stomatal number, length, and distribution have been shown to depend on numerous genes, one investigator (Tavcar) hypothesizing at least three pairs.

Genes which seem to act specifically on the leaf number at least eight, among the more important being those that produce the recessive, liguleless, glossy, narrow, and crinkly variations.

The maize inflorescence, both staminate and pistillate, is particularly susceptible to genetic modification, for in this category there are at least fifteen distinct genes operating. Some of these not only cause sterility, but at least seven (an, te, $ts_{1-5}$) modify the sexual organs directly, producing andromonoecious types or wholly female plants. Arguing from this array of sexual variations, Emerson has concluded that the expression of sex in plants is quite similar genetically to any other complex hereditary character, and accordingly that the mere modification of sex characters environmentally does not dispose of the chromosome theory of sex determination.

Row number (of kernels) on the maize ear is a typical quantitative character, presumably governed by multiple factors. I have recently been able to demonstrate the existence of some of these factors that determine row number. This has been done by proving that linkage is found between simple, qualitative factors, (such as cob, aleurone, and endosperm color, and endosperm texture) and number of rows. The experimental evidence indicates that on four different chromosomes at least, there exists something that modifies row number. Very likely this something is a gene, since typical linkage data occur in a very large series of crosses involving the simple qualitative genes and some of the row number factors.

Root characters have been little studied, for obvious reasons. The one type known is very distinct, rootless being characterized by the failure of the secondary roots to emerge or develop.

The endosperm of maize seems to be particularly susceptible to genetic modification. The complex carbohydrate development in this tissue is clearly governed by a rather simple, hereditary set of genes, as the sugary, waxy, and floury genes. The cell development of this endosperm is controlled by a very large series (at least 16) of distinct, recessive genes which

TABLE 1

*Outline of hereditary characters in maize*

I. GENERAL PLANT
- Teopod—Tp
- Plant height (dwarfs)
  - dwarf—$d_1$–$d_5$–$d_8$
  - brachytic—br
  - brevis—bv
  - nana—na
  - tiny—tn
  - anther-ear—an
- Stomata (3)
  - number
  - length
- Suckering—?
  - zig-zag stalk—$zg_1$–$zg_2$

II. LEAF
- Adherent—ad
- Blotched—bl
- Crinkly—cr
- Dead margin—dl
- Frayed—fr
- Glossy—$gl_1 \cdots gl_4$
- Liguleless—lg
- Narrow—nl
- Slashed—sl
- Twisted—$tw_1 \cdots tw_4$

III. INFLORESCENCE
- Anther ear—an
- Barren—ba
- Barren-sterile—bs
- Coherent tassel—co
- Fasciated ear—fs
- Male sterile—ms
- Naked—nk
- Pod—Tu
- Proterogyny—
- Ramosa—ra
- Row number—?
- Silkless—sk
- Tassel ear—te
- Tassel seed—$ts_1$–$ts_4$
- Weak tassel—
- Sorghum tassel—sg

IV. CHEMICAL OR PHYSIOLOGICAL
- Diabetic—glu (glucostacty)
- Disease resistance—
  - smut
  - rust
- Lazy—la (lacks lignin)

V. ROOT
- Rootless—rt

VI. GAMETE
- Gamete—Ga
- Pollen-ovule abortion

VII. EMBRYO
- Abortive—ab
- Germless—$gm_1$–$gm_2$
- Miniature germ—mg
- Premature germination—ge

VIII. ENDOSPERM
- Defective—$(d_2 \cdots d_{18})$
- Floury—fl
- Pseudo-starchy—3
- Sugary—su
- Scarred—sc
- Shrunken—sh
- Waxy—wx

IX. CHLOROPHYLL PIGMENTS
- Albino—$w_1 \cdots w_{10}$
- Argentia—ar
- Aurea—$au_1$–$au_2$
- Fine streaked—fi
- Fine striped—$f_1$–$f_2$
- Golden—$g_1$–$g_2$
- Green stripe—gs
- Iojap—ij
- Japonica—j
- Lineate—$li_1$–$li_2$
- Pale-green—$pg_1 \cdots pg_3$
- Piebald—$pb_1 \cdots pb_4$
- Polka-dot—pk
- Striate—$st_1$
- Virescent—$v_1 \cdots v_{10}$
- White-base—wl
- White-sheath—ws
- Yellow seedlings—$l_1 \cdots l_4$
- Yellow-green—yg
- Yellow-stripe—ys
- Xantha—$xn_1 \cdots xn_2$
- Zebra—$zb_1$–$zb_2$

X. GENERAL PIGMENTS (anthocyanin and flavone)

*Aleurone*
- General anthocyan—$A_1$–$A_2$–C–R
- Purpling—Pr
- Inhibitor—I
- Intensifier—in
- Spotting—S
- Blotch—Bh
- Brown—Bn

*Endosperm proper*
- Yellow—$Y_1$–$Y_2$–Yp
- Dominant white—Wh

*Pericarp-cob*
- Pp—(multiple allelomorph series)—
- Brown—Bd–bp
- Cherry—$r^{ch}$

*Plant color*
- General anthocyan—$A_1$–$A_2$–$R^r$–$R^g$
- Purple anthocyan—Pl
- Brown (Intensifier)—B (flavone)
- Silks salmon—sm
- Brown midrib—bm
- Midcob color—Md

*Scutellum and plumule*
- Purple—Pu

prevent normal development of endosperm tissue. The embryo itself is occasionally affected by genes, such as those producing germless seeds, premature germination, and the like.

Chlorophyll content in maize exhibits the genetic complexities so characteristic of the chemistry of this pigment itself. At least 67 genes have been isolated that control the formation or development of chlorophyll. Some of these genes are concerned with the green components, others with the yellow components of chlorophyll, while still others affect the vires-

cence and the pattern or distribution of the pigment. For the physiologist the stage is now well set for a critical study of the maize chlorophyll pigments since the geneticist can isolate the various pigments in a pure state, genetically.

The anthocyanin or flavone pigments and others of a similar nature have been subjected to a great deal of genetical investigation. Aleurone color is known to be dependent on at least ten different genes. The yellow and colorless endosperm pigments have not been satisfactorily analyzed as yet although we know of at least four genes acting here. The pericarp or cob pigments afford an excellent example of multiple allelomorphs, there being at least twelve allelomorphs involved. The general anthocyanin and flavone pigments in the leaf and stalk have been well analyzed by Emerson, and some seven controlling genes isolated.

This very brief summary of the known types of hereditary characters in maize should indicate that every portion of the plant is subject to genetic modification by what we call Mendelian genes. The total number of known genes is difficult to estimate, but a rough approximation would place the number at 180 or more.

The isolation of this relatively large number of genes has of course eventually resulted in the discovery that two kinds of inheritance are at work in maize, the independent and the linked types. The number of linkage groups is not yet definitely established, which is not surprising in view of the tremendous number of combinations involved where ten groups are expected. At present there are ten provisional groups.

Through the courtesy of Dr. R. A. Emerson, in whose laboratory a recent summary of linkage in maize has been prepared, I can present the latest information on these ten groups in a diagram giving a general idea of the present status of this phase of maize genetics (fig. 1)[2].

The details of this chromosome map are not of particular interest to the general botanist. However, I might call attention to the distribution of the various types of genes found on the ten chromosomes.

There is no evidence that any one chromosome carries most or all the genes for a specific plant character. On the contrary there seems to be a random distribution of the genes. For example, if we analyze some of the more important parts of the plant, we find that the genes for certain characters occur on many of the chromosomes, as follows:

| | |
|---|---|
| General plant height (dwarfs) | —on 5 different chromosomes |
| Leaf variations | —on 5 " " |

[2] More recent evidence from the Wisconsin and Cornell laboratories shows that linkage groups IX ($d_1-pg_2$) and X ($A-ts_4$) belong together. There is also evidence that a new pericarp factor belongs in a tenth group.

| | | | |
|---|---|---|---|
| Inflorescence variations | —on 5 | different | chromosomes |
| Embryo variations | —on 3 | " | " |
| Endosperm variations | —on 4 | " | " |
| Chlorophyll variations | —on 9 | " | " |
| Anthocyanin and flavone colors | —on 8 | " | " |

Factor interactions should afford a very instructive insight into the nature of gene action. It may perhaps be questionable whether we are ready to generalize in this matter, however. Nevertheless, in maize we have discovered practically all the common interrelations between factors. To the geneticist, this is expressed in terms of the 9:7, 15:1, 13:3, 12:3:1, and 9:3:4 $F_2$ ratios, characteristic of the interplay between genes when two or more pairs interact. The 9:7 type of interaction, representative of complementary action, is by far the most common. A few inhibitors are known (expressed in a 3:13 ratio). One may say that remarkably fewer 15:1 (or 63:1) interactions occur in maize than in other grasses, particularly wheat and oats. To me this has always signified a different chromosome origin in the two types of genera, and I conclude that the ten chromosomes of maize have been the basic or haploid number for a long period of time, whereas in wheat and oats the common forms with 42 chromosomes are presumably hexaploid fundamentally; which means that in the past there have been more than the two normally homologous chromosomes in the species, subject to similar gene mutations. In other words, evolution here may have progressed by chromosome doubling, followed by mutations in chromosomes that were once homologous but are no longer so.

Mutation phenomena in maize have offered the greatest field of activity in the newer genetics. In the last ten years there has been a great expansion in the number of inbred lines of corn derived from self-fertilization. This has not only uncovered hundreds of recessive mutants already in existence, but has proven that gene mutations do occur under our eyes in pedigreed cultures. Where a highly inbred line has been under critical observation for five or more years, it is possible to prove that hereditary variations which occur are actually new mutations in the true sense of the word. Practically every investigator has noted the occurrence of new mutations in maize within the last 8–10 years.

Stadler has recently subjected controlled, pedigree cultures of maize to critical tests of mutation frequency, using very ingenious methods to obtain enormous numbers in these experiments. Dealing with the well known aleurone-color genes *A*, *C*, *R*, *Pr*, and *I*, as well as with the endosperm-texture genes *Sh*, *Wx*, and *Su*, he has found recessive mutations in all except the *Wx* gene, where a test involving 1,500,000 gametes uncovered none.

The frequency of mutation varied greatly among these eight genes. The *R* gene proved to be the most mutable, with an average rate of four per 10,000 gametes. However, the same gene varied greatly in different stocks, one showing a rate of 21.7 per 10,000 gametes.

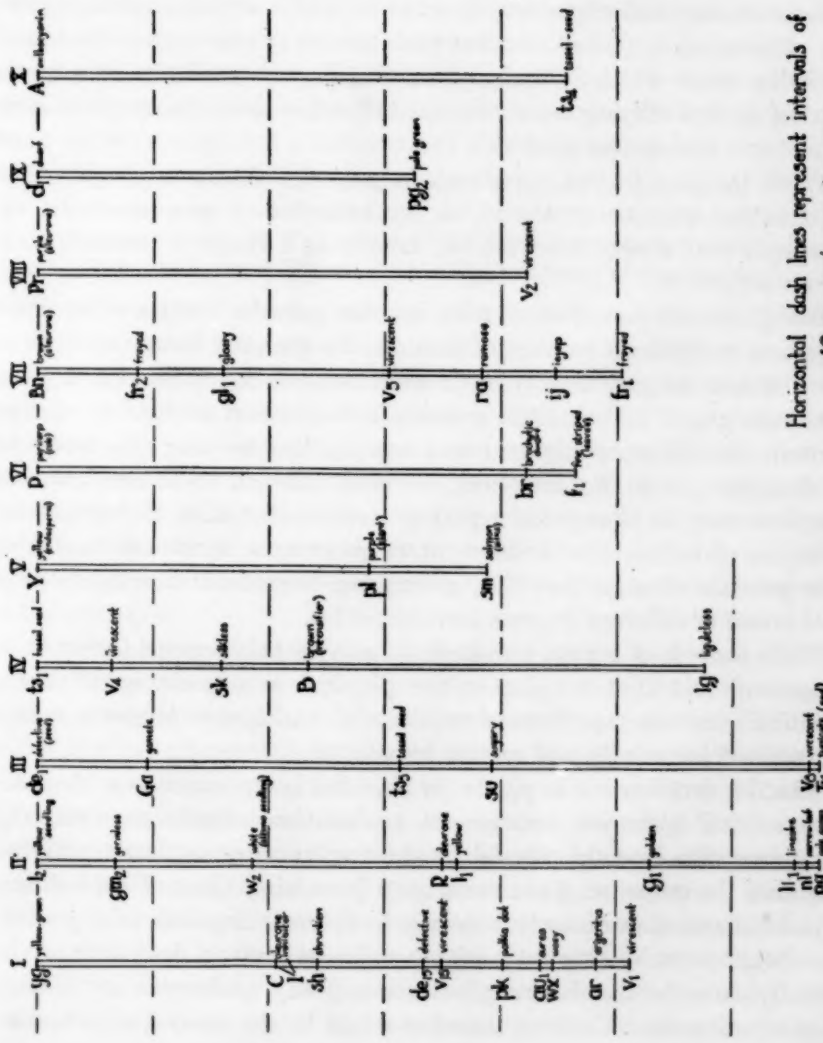
These mutations are of course strictly gene mutations, and once formed, they exhibit typical Mendelian heredity, uncomplicated by chromosome irregularity. As far as is known, there is no apparent causal agent operating in their production. We merely say that they are 'natural' mutations, produced by some internal change.

In contrast to these we have the artificially induced mutations in maize. Stadler has provoked gene mutations by X-ray treatment of pollen, seed, and very young embryos (within 24 hours after fertilization). He reports that about 30 induced mutations for seedling characters appeared, some already known, as well as several not reported previously. The rate of mutation for these seedling characters was nearly 5 per cent with the heaviest treatment. He seems to have evidence that these are actually gene mutations and not chromosomal disturbances.

The X-ray treatments also affect the chromosomes directly, either causing a translocation, a deficiency in a portion of a chromosome, or even the loss of an entire chromosome, presumably by non-disjunction. In Stadler's work, the evidence for such chromosomal disturbances rests upon genetic evidence, such as the causation of a particular form of sterility (well explained by translocation), by the appearance of mosaics (of seed characters) involving linked genes, and by the appearance of recessive characters which normally should be covered by their dominant allelomorphs. The data on seed-mosaic production showed that these were produced 20 to 40 times more frequently by X-ray treatment than under natural conditions.

The time of application of the X-ray treatment in the life history of the plant and the comparative effects of such treatments at various stages, offer the embryologist or morphologist unrivaled opportunities for investigating the actual cellular development in the ontogeny of the maize plant from the fertilized egg to the mature sporophyte.

Closely associated with such mutation phenomena are the investigations of the very mutable variegation genes in maize. Emerson has demonstrated with reasonable certainty that a particular locus on the sixth chromosome which bears the pericarp-cob color genes undergoes very frequent somatic and germinal mutation from recessive variegated to dominant self-color (red or brown) pericarp. He has determined that this gene mutates 2.7 times more frequently in the heterozygous stage than in the homozygous. The rate of mutation of this variegation gene has been



Horizontal dash lines represent intervals of 10 per cent crossing over

Fig. 1. Provisional chromosome map of maize, 1929.

determined, but because the rate varies so during the period of ontogeny in pericarp development, its precise evaluation is not of interest to the layman.

Recent studies (Emerson) have shown that the mutation rate of the variegation gene is influenced by something of a genetic nature that is carried even in colorless-pericarp strains of maize, a very interesting situation. Emerson's hypothesis is that such strains (white maize) introduce modifying genes which influence the mutability of the variegation gene, and that such modifying factors are carried on the same chromosome with the mutable variegation gene.

While the data fit this hypothesis in general, it is not impossible that the situation may be explained on the behavior of gene elements, an hypothesis that Eyster has evolved, largely as a result of research with maize variegation.

Briefly, Eyster conceives of a variegation gene (or certain other color genes) as comprising a number of particles for pigment formation (called gene elements or genomeres) of at least two sorts. Whenever a gene reproduces at cell divison these genomeres may assort at random to give different proportions of pigment and non-pigment forming genomeres in the daughter genes. By selection, the proportion of these two sorts of genomeres may be changed in a plus or a minus direction, giving various intensities of color. The assortment of genomeres in mitosis may also cause somatic changes in color, giving rise to somatic mutations (sectorial areas) of different degrees and intensities.

While there is of course, no physical basis for this concept (other than the general fact that nothing in the physical or organic world seems indivisible), certain experimental results with variegation phenomena can be explained reasonably well on this hypothesis.

Selective fertilization in plants (or animals) is a phenomenon that deserves critical attention because its explanation affords an unusually basic perception into the physiological interplay of protoplasm in higher organisms. In maize we have some very promising cases of such differential fertilization, due largely, it seems, to differential pollen tube growth. Jones began some of this work with a series of tests to determine if the naturally cross-fertilized corn plant showed any preference for foreign pollen over its own. Contrary to what might be the general expectation, he found that the individual maize plant, when double-pollinated with its own and with foreign pollen, favored the former. Practically all pollen mixtures showed a slight selective action in favor of the plant's own pollen. This was attributed to the different rates of growth of the two sorts of pollen as may be determined by comparing the results of the fertilization in the upper and lower halves of the ear.

Such an occurrence has been found to explain many cases where Mendelian ratios deviated significantly from what was expected. This was first investigated in maize when the simple 3:1 ratios of starchy and waxy (*wx*) endosperm did not conform. Brink has shown that this exception rests on differential pollen tube growth. He has gone further to demonstrate a greatly increased difference in fertilization by *Wx*- and *wx*-containing pollen when the recessive sugary gene is involved in the staminate parent. His results from certain backcrosses where 50 per cent waxy seeds are expected may be shown clearly as follows:

♀ wx wx su su × Wx wx Su Su = 2% deficiency of waxy seeds
♀ wx wx Su Su × Wx wx Su Su = 2% deficiency of waxy seeds
♀ wx wx su su × Wx wx su su = 15% deficiency of waxy seeds
♀ wx wx Su Su × Wx wx su su = 15% deficiency of waxy seeds

From this Brink argues that the pollen tube growth is greatly stimulated (or retarded) only when the staminate parent is carrying the sugary genes, *su su*. The hypothesis advanced is that 'the cytoplasm contributed by the sporophyte to the microspores is different in sugary and non-sugary plants; and that for some reason, not at present known, waxy gametophytes receiving sugary-type cytoplasm are handicapped in development. It is suggested that the two classes of male gametophytes, waxy and non-waxy, grow in the style at different rates during the period in which they are dependent upon the pollen (food) reserves and thereafter at the same rate.'

Correns, Emerson, and Jones have each reported a very similar case in which sugary and non-sugary ratios were abnormal. Their experiments center around crosses involving rice pop-corn varieties which introduce something into crosses with sweet corn that causes differential fertilization. Mangelsdorf and Jones as well as Emerson have advanced an hypothesis that this something is traceable not directly to a physiological interaction between style and pollen tube because of carbohydrate differences, but to a dominant gene, *Ga*, operating in the male gametophyte. This gene is thought to be carried on the same chromosome with sugary, and to express its effect in the gametophyte generation by stimulating the rate of pollen tube growth. On this same chromosome is borne a defective-endosperm gene, $de_1$, which also is affected by *Ga*. Both *su* and $de_1$ are shown to be affected, and cases are given where there is an excess as well as a deficiency of both recessives in hybrid generations, a phenomenon characteristic of linkage in the coupling and repulsion phases.

Recently Demerec has published some interesting results on cross sterility that have a bearing on the preceding situation. He finds that rice pop-corn is almost completely sterile with pollen of other types of

maize, including the flint and sweet varieties especially. His data show conclusively that pop-corn pollen is perfectly functional on the silks of these same varieties. This differential fertility is not due to the inability of the pollen tubes of the other varieties to compete with those of pop-corn on pop-corn silks, but it occurs because the pop-corn is sterile with this foreign pollen and fertile with its own. This he shows by pollinating the same pop-corn ear with two sorts of pollen. From this experiment Demerec is inclined to believe that causes other than differential pollen-tube growth are involved in this and similar situations.

Cyto-genetical aspects of maize are beginning to reach a stage of importance, particularly with the discovery of triploidy, occurring naturally, as well as in hybrids of maize with perennial teosinte, *Euchlaena perennis*. Miss McClintock has recently described a natural maize triploid in which ten trivalent chromosomes were frequently noted, although there was some tendency for disassociation of these trivalents at diakinesis.

Reciprocal crosses of triploid × diploid maize showed a decided selection against extra-chromosome-carrying male gametes, and a lesser selection against this in the eggs. Limited genetic data involving three pairs of genes seem to indicate that typical trisomic inheritance, in which the three homologous chromosomes assort at random, prevails ordinarily.

When maize is crossed with perennial teosinte which has 40 chromosomes (often assorting as quadrivalents) the $F_1$ hybrids possess 30 chromosomes. At least some of these show the trivalent condition at diakinesis of the hybrid, presumably two teosinte and one maize chromosome making up a set. By an ingenious set-up of linked genes, Emerson has studied the genetic results that follow from such a bigeneric cross, thus giving indirect evidence on the chromosome behavior at the reduction division.

If in this triploid $F_1$ of teosinte-maize ancestry, any three homologous chromosomes disjoin and assort at random (two going to one pole and one to the other), 50 per cent of the gametes should carry the one maize chromosome, and one sixth or 16.7 per cent of the gametes should lack teosinte chromosomes. Emerson's genetic evidence, involving four different linkage groups and hence four different chromosomes, proves conclusively that 50% of the gametes do contain the one maize chromosome. However, instead of the 16.7 per cent of non-teosinte chromosome gametes expected with random disjunction, only 7 per cent were found. This indicates that disjunction of the trivalent chromosomes in this bigeneric hybrid is not completely at random, but that the two teosinte chromosomes separate more frequently than they remain together in one daughter cell. While this differential disjunction takes place, the third homolog, or maize chromosome, is distributed at random.

Pollen and ovule sterility has recently been investigated by Brink, who reports a semi-sterile condition in which one half of the pollen grains and embryo sacs abort. Such sterility is definitely hereditary, and follows a peculiar mode of inheritance. Self-fertilization of a semi-sterile plant gives progeny of normal and semi-sterile plants in equal numbers. Reciprocal crosses between normal and semi-sterile plants produce a like result.

A provisional explanation of these peculiar genetic results is afforded by an hypothesis based on a dihybrid situation, in which the four usual gametes, AB, Ab, aB, ab, are produced but the AB and ab classes abort. The mechanism causing this abortion is thought to be a translocation of a part of a chromosome to a non-homologous chromosome. This would produce an unbalanced condition in two spores following a reduction division of a semi-sterile plant, which eventually might result in abortion.

Because of time limitation, I have not been able to discuss the tremendous number of typical Mendelian analyses that have been reported during the past decade. Research of this type, while perhaps not of first order importance, is highly essential, especially in plants, where we must test the generality of the *Drosophila*-type of heredity. This sort of investigation in maize is exceedingly laborious and time-consuming. Without it, however, advances cannot be made. Up to the present, it seems that maize follows reasonably well the same sort of inheritance that characterizes *Drosophila*, with the exception that crossing over occurs in both sexes.

This intensive study of a naturally cross-fertilized species has uncovered an astonishing amount of genetic variability in maize. This, coupled with a high rate of crossing over in most chromosomes, has resulted in a reasonable hypothesis as to why it is so difficult, if not practically impossible, to develop a homozygous genotype that possesses a good share of desirable qualities. And yet, we have no really exact and indisputable answer to the difficulties encountered in inbreeding. This awaits a more refined analysis of the genes.

Nor is there as yet a wholly satisfactory theory in explanation of heterosis. The hypothesis of dominant, linked genes answers reasonably well, but a critical verification is lacking. This also awaits a better and more detailed knowledge of the genes, particularly those governing the quantitative sort of characters.

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# The pathology of maize[1]

L. W. Durrell

As I look over the vast fields of corn in this great region, the so-called corn belt, I always think of what our forefathers said when they first beheld the corn fields of the Indian, 'It is a goodly sight.' It was not long before these men first saw corn that Sir Francis Bacon had made the startling statement, 'I take all knowledge to be my province.' Until recently one could know all about corn. Today, as manifest by this symposium, the knowledge of this great crop has diverse ramifications beyond the reach of one person. In the few minutes I have you can see that I shall only be able to review briefly the history of corn disease, and moreover, to give this review with my own interpretation.

Some of the earliest work on corn disease was that on corn smut in Illinois in the 1880's. There were numerous tests made of the feeding of corn smut to cattle to determine if it was poisonous. About this same time, 1897–98, Stewart and later Erwin F. Smith published articles on the bacterial wilt of corn. From then until about 1906–1908 little was done on corn diseases.

In 1908 Heald made studies of *Diplodia Zeae*, as also did Burrill and Barrett. In the period following the first studies on corn, corn acreage greatly increased, bringing the usual accompanying symptoms of crowding and disease; also the workers and searchers in pathology increased in number.

Piemeisel in 1917 published on the parasitism of *Ustilago Zeae*. In this paper he stated that the infection was purely local and that infection is associated with injury, close planting, late planting, and that a rich soil is conducive to smut. He found vigorous plants most susceptible. His study of the physiology of the organism was instructive. He cultured the organism, found that it did not lose its virulence when grown on artificial media, nor did the sporidia lose viability on dessication, neither did freezing injure them very much. The chlamydospores, however, were found to lose their viability in silage. He also determined their cardinal temperatures, finding that 20° to 26° C. was optimum for budding.

[1] Based on an invitation address presented in a symposium on the Biology of Maize before the joint meeting of Section G (Botany) of the American Association for the Advancement of Science, the Botanical Society of America, the American Phytopathological Society, and the American Society of Plant Physiologists at Des Moines, Iowa, 31 December 1929.

In 1921 Melchers reported on cultures of *Ustilago Zeae*, stating that different strains differed in their infection power, and he suggested physiological races. Closely following this Jones in his genetic studies showed that susceptibility to smut was governed by factors capable of segregation.

Hayes, Stakman, et al. applied their knowledge of *Ustilago Zeae* to problems of breeding for resistance. They concluded that the most promising means of controlling corn smut was by use of resistant varieties. Further, it appeared from their experiments that localization of smut on the plant, also resistance or susceptibility, was dependent upon strain characteristics. Further, only a few genetic factors seemed to be involved.

Garber and Quesenberry in 1925 published on breeding for resistance to corn smut. Immer and Christensen made further study on the inheritance of reaction to *Ustilago Zeae* and the behavior of selfed lines. Griffiths, 1928, published on the susceptibility of naturally resistant corn when artificially inoculated.

As in other fields of study, recent investigations of corn smut seem to have swung back to physiology and cytology with a different viewpoint in an effort to dig deeper into old problems with new tools. This is manifest by studies of Platz at Ames on germination and infection. He found injection by means of hypodermic needles inadequate for testing of resistance and produced infection by dropping spores in the sheath. He found a correlation between infection and the unfolding of the sheath. This perhaps answers the question as to how infection takes place. The investigations of the Minnesota laboratory and of Eddins of Ames on the physiological specialization in smut and the accompanying studies on heterothallism are of extreme interest. It would seem that these studies represent the present trend.

During the time the earlier studies of smut were being carried on a new disease was found, which for the time created considerable interest and apprehension. In 1911 Barrett discovered *Physoderma* of corn in Illinois. Several findings in various states were later reported. Tisdale made a study of the distribution of the disease and its relation to environment. Our fears were more or less allayed by his studies, since he showed that the chief center of disease was far south of the main corn belt. High temperature was necessary for its propagation, 23–30° C. being most favorable.

About 1918 intense interest was manifest in the so-called root, stock, and ear rots of corn. These were apparently considered to represent a specific disease, and much confusion and controversy centered around them. It did not become apparent at first that these rots were the result of several agencies and that we were confusing a collection of symptoms.

Even the root worms and their work were dragged into it. This is not surprising, as I remember once showing a photograph of a corn field affected by *Basisporium gallarum* to a prominent entomologist, who told me it was identical in appearance with a photograph he had of a field attacked by stalk borer.

The studies to unravel the root rot story centered first around fusarial diseases. As early as 1891 Arthur had called attention to *Gibberella*, and later Selby and Bolley had written of fusarium-sick soil. Outstanding among the more recent studies of root rot were these of Hoffer in 1918. He emphasized the selection of disease-free seed and later the relation of corn rot to wheat scab. A series of papers followed on the control of root, stock, and ear rot and their relation to the wheat scab organism.

In Iowa, Pammel, 1914 and 1916, had called attention to root-rotting of corn, but the symptoms of root rot here did not appear to be the same as those in Illinois and Indiana. The Chicago meeting in 1920 was prolific of papers on corn rots. Gilman called attention to the confusion and misinterpretation of the symptoms in different localities. Duddleston and Hoffer told us of their famous germinator. Trost and Hoffer suggested kernel starchiness as an index of susceptibility to root, stalk, and ear rots. Valleau suggested resistance as a basis of control of these rots; his work emphasized the universal infection of ear and seed with *Fusarium moniliforme*, and said that selection of disease-free seed was impossible and that he had obtained no favorable results with seed treatments. I believe it was at the same meeting that Rosen suggested a bacterial organism as a cause of root and stock rot in Arkansas.

Conclusive work was done by Dickson on the physiology of *Gibberella Saubinetti*, using the excellent equipment of the Wisconsin laboratories for the study of soil temperatures. He made a careful study of seedling blight. Though the infection was found proportional to the amount of infestation, temperature was shown to be the most important factor in seedling blight. The critical soil temperature of seedling blight of wheat was 12°C., for seedling blight of corn 20° to 24°C. Dickson found the environmental factors affecting the host to be the fundamental cause of susceptibility. Seedlings became susceptible when they were unable to respond favorably to environment. Koehler, Dickson, and Holbert made further studies of wheat scab and corn root rot caused by *Gibberella* in relation to crop succession. Their field experiments showed wheat scab was worse following corn in rotation and that root rot of corn was worse following wheat. *Gibberella Saubinetti* was the chief organism associated and proper rotation was shown to be highly advantageous. Their work also indicated that carefully selected resistant strains were less subject to the disease.

Up to 1921 and 1922 the bulk of the work on corn diseases had been confined to fusarial troubles. We were confused by symptoms and meaningless terms; the diversity of methods of germination and the interpretation of the variety of fungi on the germinator and their real meaning seemed an endless puzzle.

The problem seemed to be to separate, if possible, the causal agents and thereby the symptoms and not give the proposition a shotgun treatment. The work of the Iowa Station aimed at this. If you will pardon reference to my own studies, the reconsideration of Burrill's purple sheath spot showed that this symptom could be produced by several causal organisms, and their mode of entering and the mechanics of infection proved the key to infection studies on several other corn organisms, including *Ustilago Zeae*. Based on this principle of infection, experiments were conducted that demonstrated the importance of nodal infection and the relation of these ear and stalk rots to pollen, water, and inoculum in the sheath. In succession the intimate workings of *Diplodia Zeae* and *Basisporium gallarum* were exposed. These organisms were shown to be only semi-parasitic except under such conditions as occur in the corn sheath. The chief advance following the first *Diplodia* studies was the proof of local infection and seed injury. Soon afterward Burrilston and Holbert demonstrated the invasion of corn tissue by *Diplodia*, and Raleigh showed that this invasion was closely related to temperature, increasing with higher temperature. *Basisporium gallarum*, first recorded as a saprophyte by Artzberger, was found to be parasitic on the ears of corn, inconspicuous it is true, but being a cellulose-loving fungus it destroyed the shanks and tissues of the nodes. The results were breaking of the stalks and snapping off of ears. Structural features, such as lignification and vascular development, were correlated with the place of breaking. Reddy later showed the effect of low soil temperature on seedling infection by *Basisporium*. As by-products of these studies, a mass of unpublished data was accumulated on seedling blights which until recently have been more or less overlooked. Under the proper conditions I have seen fields of corn cut 50 per cent in stand by such common fungi as *Penicillium purpurogenum*.

The cataloguing and interpretation of the wealth of fungi found on germinating corn and their effects on the germination were also studied. Other diseases considered were the bacterial leaf spots by Kendrick. *Sclerospora graminicola* in 1921–23 was found in field surveys by Weston and later by Melhus and VanHaltern. The disease due to this fungus is not prevalent and is found only on a few plants. It has much in common with the downy mildew disease of corn in the Orient. It is extremely prevalent on the green foxtail grass in many corn fields and offers a con-

stant threat. The host range and the physiology of *Sclerospora* are at present being studied by Miss Howe of Colorado.

In this process of isolating one by one the causes of the diverse disease symptoms on corn, the work of Reddy and Holbert on the black bundle disease must be mentioned. A demonstration of so-called root rot was interrupted by finding that the diseased plants had healthy roots to the depth of an eight-foot trench. This upset the theory that had been proposed, and studies revealed *Cephalosporium acremonium* to be closely associated with the disease. The black bundle disease is characterized by a discoloration of the vascular bundles, associated with purpling of leaves and stalks and barrenness of ears (with a reduction of as much as 33 per cent yield). The disease was found to be seed-borne. It does not inhibit germination or early vigor, but materially affects grain production.

In Indiana the pendulum has swung away from root rots as originally studied to the accumulation of aluminum and iron in the corn plant and to studies of the corrective action of phosphates. At other stations tests of various seed treatments hold the stage. The use of organic mercury dusts has greatly stimulated these studies, and it is interesting in this connection that the loss to stand from the border line seed infected with *Diplodia* can be remedied by seed treatment, a thing heretofore considered possible only by laborious seed testing.

In the time allowed it is impossible to discuss all the angles of corn disease work over the last ten or fifteen years. I might in summation say that the results of our collective efforts show that corn diseases are significant and often cause 20 per cent loss. We have isolated the different diseases of corn and identified their separate symptoms, dispelling the confusion of symptoms formerly existing. Rotation, sanitation, and breeding have received emphasis from these disease studies. Our efforts have shown that the chief attack is by control of seed infection through seed treatment and in this connection mercuric dusts give promise of great effectiveness.

The entire program carried on at different stations, often under conditions of keen competition, illustrates, however, one form of modern cooperative research and what can result from it.

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## A new Miocene Cercis from Idaho and Washington

EDWARD W. BERRY

(WITH A TEXT FIGURE AND PLATE 9)

Among the many interesting plant fossils collected by Virgil R. D. Kirkham, formerly of the Idaho Bureau of Mines, during the field seasons of 1927 and 1928 and submitted to the writer for identification, is a splendid and well preserved species of *Cercis*, represented by both an abundance of leaves of all sizes, and by numerous pods. This notable addition to the flora of our western Miocene seems of sufficient importance to merit description in advance of any extended discussion of the associated forms.

The bulk of the material upon which the species is based comes from Kirkham's Station 14, which is briefly described in a recent article.[1] This locality is a short distance east of Whitebird in Idaho County. In the paper cited the distance is stated to be about 3.8 miles, although in a statement accompanying the collections it was given as 2.5 miles. In any event it is on the north side of the road where the latter turns to the northwest and leaves the creek, and cuts across the strike of several hundred feet of shales and ash beds. Additional material of the species comes from the Brickyard exposure in the city of Spokane, Washington.

Station 14 proved to be the most prolific locality in Idaho, and it has furnished the following forms:

Acer oregoniana Knowlton
Acer Florissanti Kirchner
Acer sp.
Cassia idahoensis Knowlton
Castanea castaneaefolia (Unger) Knowlton
Carpites menthoides Knowlton
Euonymus Knowltoni Berry
Fagus pacifica Chaney
Glyptostrobus europaeus (Brongniart) Heer
Fraxinus (?) fruits
Laurus grandis Lesquereux
Laurus princeps Heer
Laurus similis Knowlton
Libocedrus sp.
Liquidambar californica Lesquereux
Liquidambar fruits
Nyssa Knowltoni Berry (?)
Nyssa hesperia Berry
Ostrya oregoniana Chaney (?)
Pinus monticolensis Berry
Platanus dissecta Lesquereux
Populus Lindgreni Knowlton
Populus heteromorpha Knowlton
Quercus Chaneyi Knowlton
Quercus simulata Knowlton
Quercus Treleasii Berry
Sequoia Langsdorfii (Brongniart) Heer
Smilax lamarensis Knowlton
Sophora Alexanderi Knowlton
Sophora spokanensis Knowlton

[1] KIRKHAM, V. R. D., & M. M. JOHNSON. The Latah Formation in Idaho. Jour. Geol. **37**: 483–504. 1929.

| | |
|---|---|
| Taxodium dubium (Sternberg) Heer | Umbellularia lanceolata Berry |
| Taxodium cone | Porana sp. |
| Taxodium seed | Leaf Fungi. |

This and other Miocene localities in Idaho would undoubtedly amply repay more extensive collecting, and this is of especial importance if middle and upper Miocene and Pliocene horizons are represented, as I believe to be the case.

The new species of *Cercis*, which is the occasion for the present note, is shown in restoration in the accompanying text figure. It may be described as follows:

**Cercis idahoensis** n. sp.

(Plate 9 and figure 1)

Leaves prevailingly large, up to diameters of 14 cm., although small ones are represented. Orbicular or reniform in outline, with a prevailingly rounded apex and a wide and more or less deeply excavated cordate base. Texturally the leaves appear to have been thin but stiff. Margins entire, but they may be faintly and irregularly undulate. Petiole stout, presumably long, although no specimens show a length of more than 2 cm. Venation prominent. Midvein stout. A stout lateral primary diverges from the base of the midvein on each side; this immediately gives off a basal secondary on the outside, which may be thin and submarginal or stouter and subprimary in appearance; 2 or 3 to 10 mm. farther out the lateral primaries fork and each fork gives off, usually at acute angles, sweepingly curved secondaries; or distally the disposition and equal size of the two may more properly be called a fork. The midvein gives off three or four pair of stout secondaries at acute angles; these ascend in sweeping curves and either fork distally or give off curved tertiary branches. All ultimate endings are camptodrome very close to the leaf margin. The internal tertiaries are well marked, transversely inosculating, frequently diminishing in the midregion to form veins of quaternary magnitude disposed in isodiametric polygonal meshes, which in turn diminish to form a fine isodiametric polygonal areolation, very characteristic of the genus *Cercis* but hard to define intelligibly.

These leaves are exceedingly abundant at Station 14, where they are associated with the pods. The rather brittle matrix and the apparent brittleness of the leaves have prevented the recovery of any perfect specimens, and the margins are seldom complete. However, all sizes and all parts are represented, and some of the smaller leaves are nearly perfect.

Pods large, relatively wide, tapering gradually proximad, abruptly contracted distad to an asymmetric mucronate tip, which may be as much as 2 mm. long, ventral and dorsal sutures present, the ventral straighter than

the dorsal but more curved than in the existing pods of *Cercis*. Substance thin. Sides transversely reticulate veined; ventral wings more obliquely veined.

The fossil pods are abundant in association with the leaves but are usually badly broken. A nearly complete small pod is figured. The largest one seen, complete except at the proximal end, has a preserved length of 10.5 cm. and a maximum width of 3.25 cm. The indicated length is about 12 cm. These pods agree in all their essential features with the living pods but are less linear in profile and also much larger. They are approached

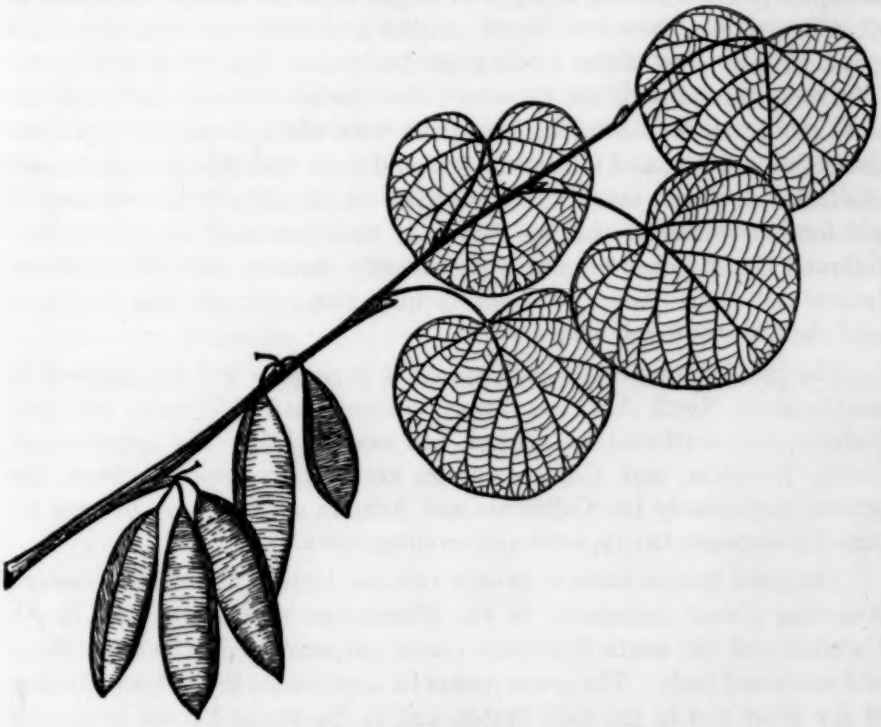

Fig. 1. Restoration of *Cercis idahoensis* Berry.

most nearly in both size and outline by the pods of the California redbud, *Cercis occidentalis* Torrey, which is usually a chaparral shrub of gravelly or rocky soils of low mountain slopes, canyons, and stream borders, found from Mendocino County and the region about Mount Shasta southward to San Diego County. Occasionally in favorable situations it reaches the size of a small tree.

It goes without saying that the species is a handsome one, and the size and abundance of both leaves and pods, and the abundant leaves of sycamore and other associated species would imply that it was an arbo-

rescent and not a shrubby form. I have compared these leaves with those of all of the existing species of *Cercis*. Only *C. canadensis* of southeastern North America and *C. chinensis* of southeastern Asia have leaves that are normally as large as the fossil. Its form is approached by the latter as well as by the European and southwestern Asiatic *C. siliquastrum*, and by the western American *C. occidentalis*. The outline and venation of *C. occidentalis* are most like the fossil but are only from one-fourth to one-third the size. Next in resemblance is *C. chinensis* with orbicular, cordate, abruptly pointed leaves, as large or larger than the fossil. The pods of *C. chinensis* are, however, much smaller and narrower than the fossil pods, in fact none of the existing species has as large or as wide pods. The most similar pods are those of *C. occidentalis* Torrey, and these are only about half the size of the fossil pods, with which, however, they agree in outline, texture, and venation. It would seem that this western American Miocene *Cercis* stood in an ancestral relationship to the existing *C. occidentalis*, which in the less favorable environmental conditions that followed the Miocene became a prevailingly shrubby form with smaller leaves and pods. Some relationship may also exist between the fossil and the Chinese *Cercis chinensis*.

The existing species of *Cercis* are eight in number and are confined to southeastern North America, Texas, Arizona, and California; southern Europe; and southwestern, central, and eastern Asia. The southeastern North American and Chinese species are small mesophytic trees, the others, particularly the California and Arizona species, have become reduced in response to dry, semi-arid environments.

The fossil species number twenty-two and include the existing eastern American *Cercis canadensis* in the Pleistocene of Canada and North Carolina and the south European *Cercis siliquastrum* in the Pleistocene of France and Italy. The genus makes its appearance in the lower Eocene of the West and in the Gulf States, and in the upper Eocene of central Europe. In the later Tertiary its distribution was Holarctic, and its post-Pliocene history has been one of progressive reduction and discontinuity in distribution. Three nominal Miocene species have been heretofore recorded from the western United States. These comprise a doubtfully determined leaf from the Esmeralda formation of western central Nevada[2] and fragments of pods from the Bridge Creek beds of the Crooked River basin in Oregon[3] and a pod fragment from the Latah formation near

[2] KNOWLTON, F. H., U. S. Geol. Survey Twenty-first Ann. Rept., Pt. 2, p. 217, *pl. 30, fig. 23*, 1900.

[3] CHANEY, R. W., Carnegie Inst. Washington Publ. 346, p. 125, *pl. 15, fig. 5*, 1927.

Spokane, Wash.[4] The only one of these at all like the Idaho species is the third, *Cercis? spokanensis* Knowlton. This was based upon a single fragment of a very small and more pointed pod. I suspect that it may represent the same species as the Idaho fossils, but nothing so small has been found in the Idaho collections, and the type is so inadequate that no positive conclusions are warranted. The pod from the Crooked River basin in Oregon clearly belongs to a different species. The small leaf from Nevada differs decidedly in venation from the minimum sized leaves of *Cercis idahoensis*. Long after the foregoing description was written E. E. Alexander of Spokane sent me the original and counterpart of a complete pod from the Latah formation which is identical with the pods of *Cercis idahoensis* except that it is somewhat smaller, but not nearly so small and much more inflated than *Cercis? spokanensis* Knowlton. This occurrence suggests that the latter was based on a small or abnormal pod of *Cercis idahoensis*, but as Knowlton's material was so incomplete that it is practically unrecognizable I do not feel justified in taking up his name for this very complete later material.

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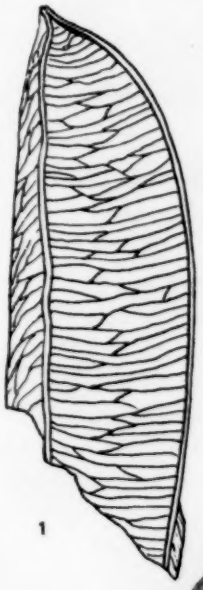
[4] KNOWLTON, F. H., U. S. Geol. Survey Prof. Paper 140, p. 43. *pl. 29, fig. 9*, 1926.

**Explanation of plate 9**

Cercis idahoensis Berry.
Figs. 1, 3. Pods from Idaho.
Fig. 2. Pod from Spokane.
Fig. 4. Leaf from Idaho.
All natural size.



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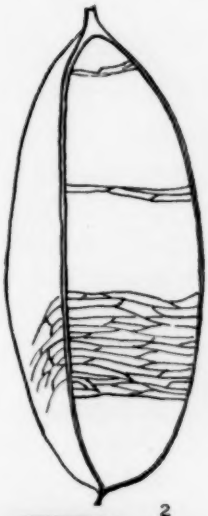

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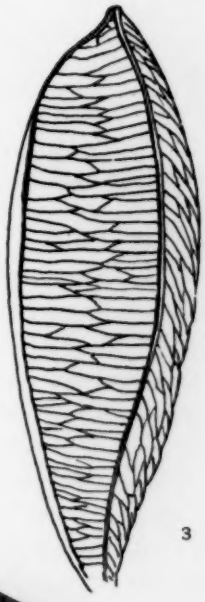

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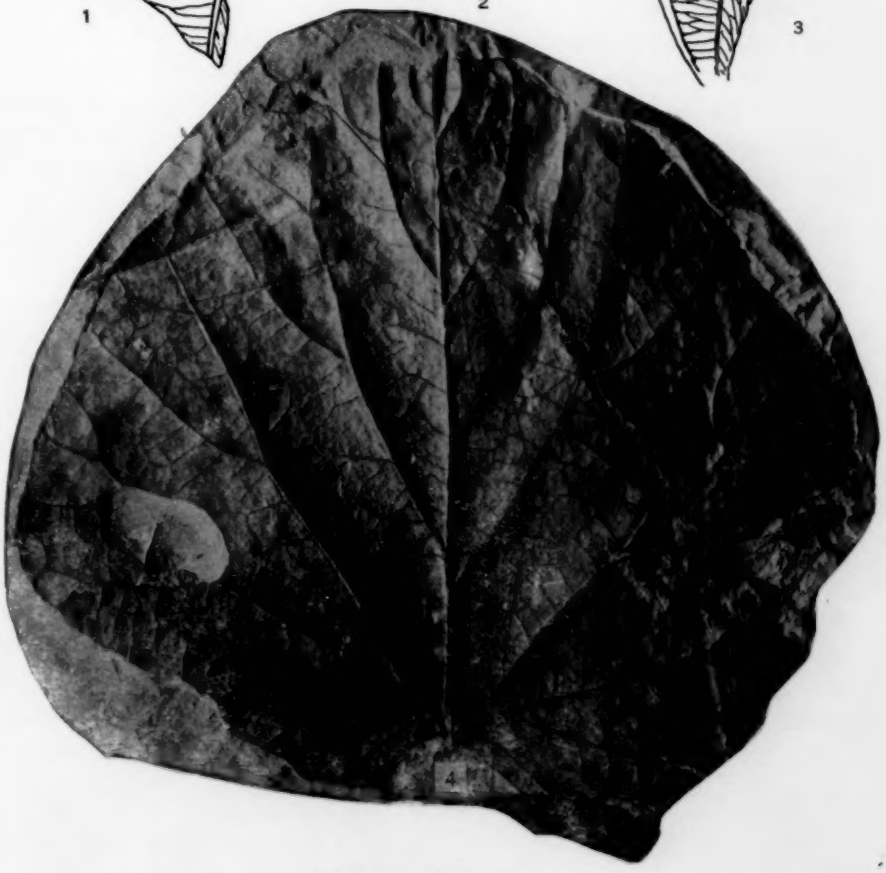

CERCIS IDAHOENSIS BERRY

UNIV. OF MICH.

# The South American species of Viburnum

E. P. Killip and A. C. Smith

At the time we prepared an account of the species of *Viburnum* occurring in northwestern South America[1] it was planned to present in a separate paper a revision of the Peruvian and Bolivian species. We have recently had the privilege of examining all of the Andean material in the rich collections of the Royal Botanic Gardens, Kew, and the Botanisches Museum, Berlin, and have found several specimens from the more northerly countries which represent species not included in our previous paper. Therefore it seems best to bring together all of the South American species in a single account. Detailed diagnoses of the species treated in the earlier paper are not repeated, although all specimens examined are listed.

The material generously lent by Kew contained the types of the species described by Oersted[2] in the genus *Oreinotinus*, which apparently have never been transferred to *Viburnum*, and which, unfortunately, were not included in our former paper. Most of the species proposed by Oersted were well marked, and their transfer to *Viburnum* becomes necessary. Oersted separated the genus *Oreinotinus* on the basis of its spuriously bi- or tri-locular fruit. It seems best, however, to consider this a well-defined subgenus of *Viburnum* rather than a distinct genus.

The Weberbauer specimens which form the bases of several of Graebner's recent species[3] were not included in the material borrowed from Berlin. From the descriptions we have been able to associate some of these species with other material with reasonable certainty; others we believe are identical with species described earlier, though not having seen the types we hesitate definitely to make the reductions.

With the exception of a single species from Mount Roraima, British Guiana, the genus *Viburnum* in South America is confined to the Andes of western Venezuela, Colombia, Ecuador, Peru, and Bolivia. A specimen of Poeppig's in the Berlin herbarium bears the inscription 'Chili?,' but in all probability this was collected in Peru. In the Flora Brasiliensis[4] it is stated that a Sello specimen from Brazil appeared to belong to a species of *Viburnum*, but the author was so doubtful that the genus was not formally included in that work. All material we have seen from southern South America clearly represents plants in cultivation.

[1] Bull. Torrey Club **56**: 265–274. 1929.

[2] Kjoeb. Vid. Medd. **1860a**: 267–303. 1861.

[3] Bot. Jahrb. **37**: 433–436. 1906.

[4] Martius. Fl. Bras. **6**[1]: 338. 1885.

By far the greater part of the specimens we have examined have been referred through casual identification to *V. glabratum* H.B.K., *V. ayavacense* H.B.K., or *V. tinoides* L.f. Although we have not seen authentic material of *V. glabratum*, the description applies to only a few of the specimens. *V. ayavacense*, of which we have seen a portion of the type, ranges from southern Ecuador to Bolivia. *V. tinoides*, common in the Eastern Cordillera of Colombia, is identical with *V. leptophyllum* Killip & Smith.

We greatly appreciate the courtesy of Dr. A. W. Hill, of the Royal Botanic Gardens, Kew, and of Professor L. Diels, of the Botanisches Museum, Berlin-Dahlem, in lending us all of their material, and thus giving us the opportunity of comparing the historic specimens of Humboldt and Bonpland, Ruiz and Pavon, Triana, and Goudot with the more recent collections of American explorers. It has also been a privilege to study the collections lent by the Gray Herbarium of Harvard University, the Field Museum of Natural History, and the Arnold Arboretum of Harvard University. The institutions from which specimens have been examined are indicated thus: Arnold Arboretum (A); Berlin (B); Field Museum (F); Gray Herbarium (G); Kew (K); U. S. National Museum (N); New York Botanical Garden (Y).

## KEY TO SPECIES

*A.* Lower surface of leaves uniformly stellate-tomentose with hairs at least 5 per sq. mm. of surface even on mature leaves.

Apex of leaves caudate-acuminate; branches of inflorescence slender (primary rays about 1 mm. in diameter) ..... 1. *V. undulatum*

Apex of leaves obtuse or acute; branches of inflorescence relatively thick (primary rays at least 1.5 mm. in diameter).

Leaf hairs straight (0.3–0.6 mm. long); fruiting corymbs wide-spreading, more than 8 cm. wide, often 13 cm.

Leaves broadly ovate or ovate-oblong (rarely a few slightly obovate); flowers in clusters of 4–6 on ultimate branches, sessile or subsessile (pedicels rarely more than 2 mm. long).

Principal nerves of leaves 3 or 4 to a side, distant (about 20 mm. apart); leaves subcordate ..... 2. *V. lasiophyllum*

Principal nerves of leaves 4 or 5 to a side, approximate (about 15 mm. apart); leaves rounded at base.

Corolla 3–4 mm. wide; calyx lobes acute or subacute; (Peru) ..... 3. *V. Weberbaueri*

Corolla more than 4 mm. wide; calyx lobes rounded; (northern Ecuador and southern Colombia) ..... 4. *V. Jamesonii*

Leaves obovate; flowers in clusters of three, one sessile, two distinctly pedicelled, the pedicels 2–5 mm. long ..... 5. *V. Goudotii*

Leaf hairs crispate (0.15–0.3 mm. long); corymbs smaller, rarely more than 10 cm. wide, usually less than 8 cm.

Leaves 12–20 cm. long, lustrous above, the nerves 5 to a side .. 6. *V. anabaptista*

Leaves up to 12 cm. long, usually dull above, the nerves 3 or 4 to a side.

Plants of lax habit, with elongate branches; inflorescence 3- or 4-times branched; leaves in twos ..... 7. *V. pichinchense*

Plants compact, the branches short; inflorescence twice-branched; leaves often in threes ..... 7a. *V. pichinchense toledense*

*B.* Lower surface of leaves essentially glabrous, sometimes pilosulous in axils of nerves (rarely, especially in *V. Urbani*, more densely pubescent, but the stellate hairs, only up to 2 per sq. mm. of surface).

Branchlets and rays of inflorescence densely canescent-pulverulent ... 8. *V. glabratum*

Branchlets and rays of inflorescence glabrous or with various indument, not canescent-pulverulent.

Leaves prevailingly broadest above middle, often in threes.

Petioles 3–5 mm. long; leaves up to 2.5 cm. wide, 3- or 4-toothed at apex; (Peru) 9. *V. tridentatum*

Petioles 6–15 mm. long; leaves more than 2.5 cm. wide; (Colombia).

Branchlets essentially glabrous; bractlets persistent, up to 7 mm. long; calyx tube densely glandular-punctate ..... 10. *V. Halli*

Branchlets rufo-tomentose; bractlets deciduous, about 2 mm. long; calyx tube at most sparingly glandular-punctate ..... 11. *V. suratense*

Leaves broadest at or below middle.

Leaves predominately in threes.

Margin of leaves entire.

Branchlets essentially glabrous; peduncles and rays of corymb finely subappressed-hirtellous; (Colombia to northern Peru) .... 12. *V. triphyllum*

Branchlets, peduncles, and rays of corymb densely stellate-tomentose; (central Peru) ..... 13. *V. Incarum*

Margin of leaves toothed, at least towards apex.

Flowers up to 5 mm. wide when expanded; leaves stellate-pubescent beneath; (Colombia) ..... 14. *V. Urbani*

Flowers more than 5 mm. wide when expanded; leaves glabrous beneath, or pubescent on principal nerves.

Leaf margin not ciliate; calyx tube eglandular; (Peru) .... 15. *V. Mathewsii*

Leaf margin slightly revolute and appearing to be regularly ciliate; calyx tube glandular; (Colombia) ..... 18. *V. fragile*

Leaves never in threes.

Base of leaves subcordate, the principal nerves 5–7 to a side; (Bolivia) ..... 16. *V. Spruceanum*

Base of leaves rounded or cuneate, the principal nerves usually 4 (rarely 3 or 5) to a side.

Corolla large, 4 mm. wide or more when expanded.

Peduncles and rays sparingly to densely hirsute, the hairs simple or with 2 or 3 branches; (Venezuela and Colombia).

Leaves glabrous above, obtuse or obtusely acuminate, entire ..... 17. *V. tinoides*

Leaves sparingly pubescent above, abruptly acuminate, denticulate towards apex, the margin subrevolute, appearing regularly ciliate 18. *V. fragile*

Peduncles and rays densely stellate-tomentose, the hairs crispate, with 6–20 branches.

Branchlets densely floccose; leaves obtusely acuminate; (Colombia) .... 19. *V. floccosum*

Branchlets essentially glabrous; leaves acute or sharp-acuminate; (southern Ecuador to Bolivia) ..... 20. *V. ayavacense*

Corolla smaller, less than 4 mm. wide even when expanded.

Leaves at least three times as long as broad; corymbs wide-spreading, 12–15 cm. wide; (Colombia).....21. *V. Toronis*
Leaves not three times as long as broad; corymbs more compact, 5–9 cm. wide (rarely up to 12 cm.).
Apex of leaves caudate-acuminate, at least 1 cm. long.
Peduncles and rays pubescent; petioles 4–8 mm. long, hirtellous; (Colombia).....22. *V. cornifolium*
Peduncles and rays glabrous; petioles 8–15 mm. long, glabrous; (Mt. Roraima).....23. *V. roraimense*
Apex of leaves obtuse, acute, or short-acuminate.
Upper surface of leaves stellate-pubescent, hairs crispate, about 2 per sq. mm. of surface; calyx tube appressed-hirsutulous.....
24. *V. divaricatum*
Upper surface of leaves glabrous; calyx tube glabrous (except in No. 25).
Hairs of branchlets and corymb dense, 0.4–0.55 mm. long; calyx tube appressed-hirsutulous.....25. *V. Lehmannii*
Hairs of branchlets and corymb sparse or dense, 0.25–0.4 mm. long; calyx tube essentially glabrous.
Margin of leaves crenate-dentate to base; (Colombia).....
26. *V. antioquiense*
Margin of leaves entire or serrate in upper half.
Leaves subsessile (petiole up to 3 mm. long), obtuse at apex; (Colombia).....27. *V. subsessile*
Leaves petioled (petiole more than 5 mm. long), acute or short-acuminate at apex.
Inflorescence mainly terminal at the ends of elongate branchlets; petioles averaging about 10 mm. in length; (southern Ecuador and Peru).....28. *V. Jelskii*
Inflorescence subaxillary as well as terminal, the corymbs borne on numerous short leafy branchlets; petioles 5–10 mm. in length; (Bolivia and southern Peru).....
29. *V. Seemenii*

## DESCRIPTIONS OF SPECIES

1. **Viburnum undulatum** (Oerst.) comb. nov. *Oreinotinus undulatus* Oerst. Kjoeb. Vid. Medd. **1860**: 288. 1861. Branchlets finely stellate-tomentose, at length glabrous; leaves lanceolate or ovate-lanceolate, 6–10 cm. long, 3–5 cm. wide, caudate-acuminate at apex, rounded, cordulate, or cuneate at base, repand-undulate, membranous, sparingly stellate-pubescent and dark green above, densely stellate-pubescent and paler beneath; corymbs 5–7-rayed, the rays very slender (about 1 mm. in diameter), densely stellate-tomentellose, 3- or 4-times branched; calyx tube 1–1.5 mm. long, the lobes orbicular, ciliate; corolla about 4 mm. wide when expanded.

VENEZUELA: Federal District: Caracas, *Linden 1669* (K).—VENEZUELA or COLOMBIA: *Linden 1128* (K, type).

2. VIBURNUM LASIOPHYLLUM Benth. Pl. Hartw. 189. 1845. *Oreinotinus lasiophyllus* Oerst. Kjoeb. Vid. Medd. **1860**: 287. 1861.

COLOMBIA: Cundinamarca: *Hartweg 1041* (K, type; B, N, fragment); *Pennell 2474* (G, Y); *Apollinaire & Arthur 76* (N); Herb. Nac. Colombia *610* (N).

3. VIBURNUM WEBERBAUERI Graebn. Bot. Jahrb. **37**: 433. 1906. Branchlets densely brownish stellate-tomentose; leaves obovate or oblong-ovate, 15–20 cm. long (or 5–10 cm. long, 4–6 cm. wide), acuminate, subentire or obscurely dentate, sparingly to densely short-tomentose above, densely tomentose, often pilose on the nerves, beneath; corymbs wide-spreading, rays 5–7, somewhat curved; calyx lobes deltoid, acute or subacute, sparsely pilose; corolla 3–4 mm. wide when expanded.

Type locality: Monzon, alt. 1600–1800 m., Huánuco, Peru (*Weberbauer 3561*).

PERU: Cajamarca: Cutervo, alt. 2300 m., *Weberbauer 7129* (B, N, Y). Tabacónas Valley, 1600 m., *Weberbauer 6241* (F, N, Y). Huánuco: Between Huánuco and Pampayacu, *Kanehira 231* (F). The leaves of these collections are much under the dimensions given by Graebner, but their general shape and indument agree well with his description. The species bears a strong resemblance to the following.

4. **Viburnum Jamesonii** (Oerst.) comb. nov. *Oreinotinus Jamesonii* Oerst. Kjoeb. Vid. Medd. **1860**: 288. 1861. Shrub 5–6 m. high; young branchlets densely stellate-villose; leaves ovate-oblong or obovate, 5–10 cm. long, 3.5–6 cm. wide, short-acuminate at apex, rounded at base, subentire or undulate-denticulate (teeth callose-thickened), sparsely stellate-pubescent above, densely stellate-tomentose beneath; peduncles stout, about 3 mm. in diameter; corymbs 6–9-rayed, 7–9 cm. wide, the flowers subsessile in dense clusters.

COLOMBIA: Nariño: 'province of Pasto,' *Jameson 433* (K, type). Tuquerres, *André 3178* (K). Without locality, *André K1090* (K).

5. **Viburnum Goudotii** nom. nov. *Oreinotinus furcatus* Oerst. Kjoeb. Vid. Medd. **1860**: 284. 1861; not *Viburnum furcatum* Blume (1858). Branchlets densely stellate-villose; leaves obovate or oblanceolate, 5–9 cm. long, 3.5–4.5 cm. wide, obtusely apiculate at apex, rounded or subcuneate at base, repand-denticulate throughout with callose-thickened teeth, coriaceous, stellate-hirsute on midnerve and sparingly so on surface above, densely stellate-hirsute beneath, nerves 5 to a side; corymbs about 10 cm. wide, the primary rays about 6, barely 1.5 cm. long, the flowers in clusters of three, one sessile, two pedicelled, the pedicels 2–5 mm. long.

COLOMBIA: Cundinamarca: near Bogotá, *Goudot 2* (K, type).

6. VIBURNUM ANABAPTISTA Graebn. Bot. Jahrb. **37**: 435. 1906. *Oreinotinus ferrugineus* Oerst. Kjoeb. Vid. Medd. **1860**: 286 (err. typ. 386). 1861. *Viburnum ferrugineum* Donn. Sm. Enum. Pl. Guat. **1**: 16. 1889; not *Viburnum ferrugineum* Raf. (1838). *Viburnum rhytidophyllum* Graebn. Bot. Jahrb. **37**: 435. 1906, as synonym; not *Viburnum rhytidophyllum* Hemsl. (1888). Branchlets stout, finely appressed stellate-tomentellous, scabrid, at length glabrous; leaves ovate-oblong, 12–20 cm. long, 5–8 cm. wide, acuminate at

apex, rounded at base, shallowly denticulate throughout with callose teeth, thick-coriaceous, prominently veined below, sparingly short-tomentose (or glabrous?) above, densely ferruginous-tomentose beneath; corymbs 3- or 4-rayed, 8–10 cm. wide, densely stellate-tomentose, scabrid; calyx tube short-turbinate, 1–1.2 mm. long.

Type locality: Colombia, without locality, *Triana*.
COLOMBIA: Antioquia: Alto San José, alt. 2700 m., *Kalbreyer 1616* (B, K).

These Kalbreyer specimens are strikingly different from all other specimens which we have examined. The leaves are unusually large, thick, and strongly nerved. We have not seen the type of *Oreinotinus ferrugineus* Oerst., but the Kalbreyer specimens agree well with the description of that species except that indument is almost completely lacking on the upper surface of the leaves, and the peduncles are about three times longer than noted in the description.

Donnell Smith transferred Oersted's name *O. ferrugineus* to *Viburnum*, applying it to a Guatemalan plant. This plant agrees in certain details with Oersted's diagnosis, but on the whole the Kalbreyer collection (which comes from Colombia, where the type of *O. ferrugineus* was collected) corresponds more fully with the description.

In applying the name *Viburnum anabaptista* to this species, Graebner cites an Ecuador collection of Lehmann (no. 7940); this we identify as *Viburnum pichinchense*.

7. VIBURNUM PICHINCHENSE Benth. Pl. Hartw. 188. 1845. *Oreinotinus pichinchensis* Oerst. Kjoeb. Vid. Medd. **1860**: 287. 1861.

COLOMBIA: Antioquia: *Jervise* (K). El Cauca: *Pennell & Killip 7383* (G, N, Y); *Lehmann 831* (N), *3548* (N), *7941* (F).
ECUADOR: Mt. Pichincha, *Hartweg* (K, type; N, fragment). Cuenca, *Lehmann 7940* (K).
BOLIVIA: Tunari, alt. 2600 m., *Kuntze*, in 1892 (N, Y).

We are unable to distinguish the Bolivian specimen above cited from material collected farther north. Flowers are lacking, and the extension of the range of the typical form is possibly not justified.

7a. VIBURNUM PICHINCHENSE TOLEDENSE Killip & Smith, Bull. Torrey Club **56**: 268. 1929.

COLOMBIA: Norte de Santander: *Killip & Smith 20589* (type), *19911, 20107, 20184, 20615* (all A, G, N, Y).

8. VIBURNUM GLABRATUM H.B.K. Nov. Gen. & Sp. **3**: 428. 1818. *Viburnum glabrum* Willd.; Schult. Syst. **6**: 639. 1820. *Oreinotinus glabratus* Oerst. Kjoeb. Vid. Medd. **1860**: 290. 1861.

COLOMBIA: without locality, *Triana 1873* (B). Cundinamarca: *Pennell 1760* (G, N, Y); *André K443* (K), *K444* (Y), *1569* (K), *1723* (K). Huila: *Rusby & Pennell 955* (G, N, Y). Tolima: *Hazen 9536* (G, N, Y); *André K445* (F, Y).

A large part of the Andean material has been referred to this species. The description of the indument of the type specimen as 'tenuiter canescenti-pulverulentes' applies only to a small number of the specimens examined.

9. **Viburnum tridentatum** sp. nov. *Oreinotinus obovatus* (R. & P.) Oerst. Kjoeb. Vid. Medd. **1860:** 286 (err. typ. 386). 1861, without description. *Viburnum obovatum* R. & P.; Oerst. Kjoeb. Vid. Medd. **1860:** 286 (err. typ. 386). 1861, as synonym; not *Viburnum obovatum* Walt. (1788).

Much-branched shrub or small tree, the branchlets slender, densely and softly stellate-tomentose; petioles 3–5 mm. long, pubescent as the branchlets; leaves in threes, obovate or narrowly oblanceolate, 3–5 cm. long, 1.5–2.5 cm. wide, rounded or short-triangular-acute at apex, cuneate at base, finely undulate-denticulate towards apex (teeth 3–5), sparingly stellate-pubescent with crispate hairs on nerves and veins both above and beneath, the secondary nerves 3 or 4 to a side, parallel, strongly ascending; peduncles 3–4.5 cm. long, about 2 mm. in diameter, densely and softly stellate-tomentose; corymbs bracteate (bracts linear, about 3 mm. long, soon deciduous), 4–7 cm. wide at anthesis, 6–7-rayed, 2- or 3-times branched, pubescent as the peduncle, bracteolate, the bractlets filiform, about 2 mm. long; calyx tube turbinate, 0.5–1 mm. long, sparingly glandular-punctate, glabrous, the lobes suborbicular, 0.5 mm. long, densely ciliate; corolla about 5 mm. wide when expanded, the lobes ovate.

Type, *Ruiz & Pavon*, collected in Peru and deposited in the herbarium of the Botanisches Museum, Berlin.

10. **Viburnum Halli** (Oerst.) comb. nov. *Oreinotinus Halli* Oerst. Kjoeb. Vid. Medd. **1860:** 292. 1861. *Viburnum apiculatum* Killip & Smith, Bull. Torrey Club **56:** 270. 1929.

COLOMBIA: El Cauca: *Lehmann 5160* (N, type of *V. apiculatum*, B, F, G).
ECUADOR: 'Cordillera towards Guayaquil, about 8000 ft.,' *Hall* (K, type).

*Viburnum apiculatum* is merely a more robust variant of *V. Halli*. In the type specimen of *V. Halli* the leaves are narrowly obovate, rarely more than 3 cm. wide, with petioles up to 7 mm. long, the peduncles are more slender, and the corymbs are about 5 cm. wide. Material recently examined of this species, as well as of *V. suratense* and *V. fragile*, has some of the leaves in threes.

11. VIBURNUM SURATENSE Killip & Smith, Bull. Torrey Club **56:** 270. 1929.

COLOMBIA: Santander: *Killip & Smith 16743* (Y, type, A, G, N), *18766* (G, N, Y). Cundinamarca: *Dawe 168* (N). Antioquia: St. Helena, alt. 2600 m., *Kalbreyer 1490* (B, K).

12. VIBURNUM TRIPHYLLUM Benth. Pl. Hartw. 189. 1845. *Oreinotinus triphyllus* Oerst. Kjoeb. Vid. Medd. **1860:** 290. 1861. *Oreinotinus laurifolius* Oerst. Kjoeb. Vid. Medd. **1860:** 291. *pl. 6, f. 11–17.* 1861; not *Viburnum laurifolium* of other authors.

This species is very variable in the shape of the leaves. The following specimens are typical:

COLOMBIA: without definite locality: *Triana 1872* (B). Cundinamarca: *Hartweg 1040* (K, type, B, Y); *Pennell 2006* (Y); *Dawe 156* (N); *Bro. Ariste Joseph A501* (N), *B106* (N); *Goudot 1* (K); *Tracy 85* (K). Antioquia: *Lehmann CCXV* (N). El Cauca: *Pennell 7102* (G, N, Y); *Killip 6804* (N). Nariño: *André K446* (K); 'province of Pasto,' *Jameson 484* (K).

ECUADOR: without definite locality: *André K1089* (K); *Jameson* (N). Carchi: *Hitchcock 20940* (G, N, Y). Pichincha: Quito, *Jameson* (K). Loja: *Rose 23097* (G, N, Y); *Hitchcock 21561* (N). Tungurahua: Baños, *Spruce 6104* (K). Azuay: *Jameson* (K, N).

PERU: without definite locality: *Mathews 2027*, in part (K), *2038* (K). Amazonas: *Mathews 1623*, in part (K, type of *Oreinotinus laurifolius*), *2114* (K).

We are unable to distinguish *Oreinotinus laurifolius* from typical Colombian *V. triphyllum*. Most of the specimens of *V. triphyllum* and its forms have the leaves predominately in threes. The value of this as a diagnostic character may be over-emphasized. All these specimens are characterized by the appressed-hirtellous indument of the peduncle and corymb rays.

Three forms may be recognized:

a. **Viburnum triphyllum f. macrophyllum** (Oerst.) comb. nov. *Oreinotinus triphyllus macrophyllus* Oerst. Kjoeb. Vid. Medd. **1860:** 290. 1861. Plant robust; leaves up to 12 cm. long and 6 cm. wide.

COLOMBIA or VENEZUELA: *Linden 1331* (K, type of *Oreinotinus triphyllus macrophyllus*).

b. **Viburnum triphyllum f. lanceolatum** f. nov. Leaves lanceolate or oblanceolate, at least three times as long as broad, 10–13 cm. long, 3–3.5 cm. wide.

Type, *Ruiz & Pavon*, collected in Peru and deposited in the herbarium of the Botanisches Museum, Berlin. One of the specimens under *Mathews 2027* perhaps should be placed here. The name *lanceolatum* is taken from the label of the collectors.

c. **Viburnum triphyllum f. microphyllum** f. nov. Leaves prevailingly obovate, small (1.5–3 cm. long, 0.7–1.5 cm. wide); corymbs small (up to 3 cm. wide).

Type, *Mathews 2114*, in part, collected at Chachapoyas, dept. Amazonas, Peru, and deposited in the herbarium of the Royal Botanic Gardens, Kew. Other collections from the same locality are: *Mathews 1623*, in part (K), *3099* (K).

13. VIBURNUM INCARUM Graebn. Bot. Jahrb. **37**: 435. 1906. Shrub or much-branched tree 3–5 m. high, the younger branches, peduncles, and rays of inflorescence densely stellate-tomentose; leaves usually in threes, ovate or oblong-ovate, 4–7 cm. long and 1.5–3.5 cm. broad, subacute at apex, subacute or rounded at base, entire or nearly so, minutely stellate-pubescent on nerves above, pilosulous in axils beneath; corymb up to 9 cm. wide, the peduncle about 6 cm. long, the rays 5–7; calyx lobes fimbriate; flowers about 5 mm. wide when expanded; fruit ovoid, about 8 mm. long, 5.5 mm. wide.

Type locality: Huacapistana, alt. 1800 m., dept. Junín, Peru (*Weberbauer 1986*).
PERU: Junín: Huacapistana, *Killip & Smith 24137* (N, Y), *24326* (N, Y), *24508* (N, Y).

14. VIBURNUM URBANI Graebn. Bot. Jahrb. **37**: 435. 1906. Shrub or small tree, the branches elongate-scandent, the branchlets densely stellate-hirsute; leaves often in threes, ovate, oblong, or obovate-oblong, up to 10 cm. long, 4.5 cm. wide, acuminate at apex, rounded at base, denticulate above middle, thick-coriaceous, sparingly stellate-pubescent above, more densely so beneath (hairs less than 2 per sq. mm.); peduncles stout, 4–5 cm. long; corymbs up to 6 cm. wide, 4–5-rayed, 2- or 3-times branched, the flowers 5–7 in a cluster; calyx lobes oblong, nearly as long as the tube; corolla 4–5 mm. wide when expanded.

COLOMBIA: El Cauca: Popayán, alt. 1300–1600 m., *Lehmann 5161* (B, type, K).

Examination of the type specimen, of which previously we had seen only a photograph, leads to the conclusion than *V. Urbani* is distinct from *V. pichinchense*. The inflorescence is more compact, with fewer rays, and the calyx lobes are more elongate, nearly equaling the tube. The pubescence on the under surface of the leaves, although quite evident, is scantier than in the case of species of the first division of our key.

15. **Viburnum Mathewsii** (Oerst.) comb. nov. *Oreinotinus Mathewsii* Oerst. Kjoeb. Vid. Medd. **1860**: 291. 1861. ?*Viburnum fur* Graebn. Bot. Jahrb. **37**: 434. 1906. Small tree; branchlets, peduncles and rays stellate-tomentose, the branchlets at length glabrous; leaves usually in threes, ovate to ovate-lanceolate, 3–12 cm. long, 2–6 cm. wide, rounded or acuminate at apex, rounded or subcuneate at base, callose-denticulate or subentire at base, coriaceous, lustrous and glabrous or sparingly stellate-pubescent above, glabrous beneath or stellate-pubescent on principal nerves; corymbs 5–9 cm. wide, 5–7-rayed, the rays up to 5 cm. long; calyx tube glabrous, glandular, the lobes oblong or ovate-oblong.

PERU: Cajamarca: Cutervo, *Jelski 359* (B). Amazonas: 'Bagasan', *Mathews 1605* (K, type). Huánuco: Mito, 2800 m., *Macbride & Featherstone 1385* (F), *1460* (F), *1653* (F, N), *1749* (F), *Macbride 3400* (F, G); Pozuzo, 3100 m., *Macbride 4779* (F).

The fine series obtained by Macbride permits a more complete description of this little-known species, the type specimen having consisted only of a small branchlet with depauperate leaves. Macbride's notes describe the plant as a small tree up to 5 meters high, unbranched as far as a meter from the top, the flowering branches elongate.

*Viburnum fur*, based on *Weberbauer 3895*, from the Department of Cajamarca, seems scarcely distinguishable from *V. Mathewsii*, though we have not seen the type specimen. *Jelski 359*, with thinner leaves and glabrous branchlets, may represent a new species, but more probably it is merely a juvenile stage of *V. Mathewsii*.

16. VIBURNUM SPRUCEANUM Rusby, Bull. N. Y. Bot. Gard. **8**: 121. 1912. Young branchlets sparingly appressed stellate-pubescent, at length glabrous; petioles 6–8 mm. long; leaves broadly ovate to oblong-ovate, 5–9 cm. long, 3–7 cm. wide, abruptly short-acuminate at apex, subcordate at base, entire or subentire, coriaceous, essentially glabrous above, glabrous beneath, sometimes stellate-tomentose in axils of nerves, the principal lateral nerves 5–7 to a side, close, arcuate-ascending; peduncles up to 5 cm. long, sparingly stellate-pubescent; corymbs 6–10 cm. wide in fruit, 6-rayed, pubescent as the peduncle.

BOLIVIA: La Paz: Apolo, alt. 1500 m., *R. S. Williams 2451* (Y, type, N). Rusby likens this specimen to Spruce's 6104 (cited as 5104), which we refer to *V. triphyllum*.

17. VIBURNUM TINOIDES L.f. Suppl. 184. 1781. *Oreinotinus tinoides* Oerst. Kjoeb. Vid. Medd. **1860**: 291. 1861. *Viburnum leptophyllum* Killip & Smith, Bull. Torrey Club **56**: 271. 1929.

We have recently seen an excellent photograph of the type of *V. tinoides* in the Linnaean herbarium, which is clearly *V. leptophyllum*. The typical form is represented by the following collections:

COLOMBIA: without locality, *Mutis* (type, photo, N, Y), *Jurgensen 392* (K). Santander: *Killip & Smith 17055* (N, type of *V. leptophyllum*, A, G, Y), *15864* (A, G, N, Y), *16931* (A, G, N, Y), *17059* (G, Y), *17083* (A, G, N, Y), *18869* (A, G, N, Y), *19098* (A, G, N, Y), *19226* (A, G, N, Y), *19310* (A, G, Y), *16628* (A, G, N), *16083* (A, G, N, Y). Cundinamarca: *Holton 443* (Y); *Ariste Joseph B105* (N); *Schultze 124* (N); *Triana 1870* (B).

The following form may be recognized:

**Viburnum tinoides f. venezuelense** comb. nov. *Viburnum leptophyllum f. Venezuelense* Killip & Smith, Bull. Torrey Club **56**: 271. 1929. Leaves shorter and thinner than in typical material.

VENEZUELA: Federal District and States of Galipán, Miranda, and Mérida: E. *Pittier 94* (Y, type, N); *91* (N); *Jahn 474* (N, ), *884* (N), *1058* (N); *Pittier 7406* (N), 6486 (N), *8129* (N), *12857* (A, B, N, Y); *Eggers 13575* (F, G, N), *13229* (N); *Curran & Haman 1125* (N); *Fendler 535* (G, K); *Moritz 1217* (B, G, K); *Allart 83* (N, Y); *Gehriger 333* (N, Y). Local name: 'trement .'

COLOMBIA: Santander: *Killip & Smith 15006, 15068, 15116* (all A, G, N, Y); *Karsten 32* (B).

18. VIBURNUM FRAGILE Killip & Smith, Bull. Torrey Club **56**: 271. 1929.

COLOMBIA: Huila: *Rusby & Pennell 757* (Y type, G).

19. VIBURNUM FLOCCOSUM Killip & Smith, Bull. Torrey Club **56**: 272. 1929.

COLOMBIA: Santander: *Killip & Smith 18082* (N, type, A, G, Y), *16916* (A, G, N, Y).

20. VIBURNUM AYAVACENSE H.B.K. Nov. Gen. & Sp. **3**: 428. 1818. *Oreinotinus ayavacensis* Oerst. Kjoeb. Vid. Medd. **1860**: 290. 1861. *?Viburnum Witteanum* Graebn. Bot. Jahrb. **37**: 434. 1906. Shrub 3–4 m. high; branchlets essentially glabrous; leaves ovate to ovate-oblong, 5–12 cm. long, 3–6 cm. wide, acute at apex, rounded, subcordate, or subcuneate at base, entire or obscurely denticulate, glabrous above, glabrous or sparsely stellate-hirsutulous on nerves and veins beneath; peduncles stellate-pubescent; corymbs up to 7 cm. wide, 5–7-rayed; corolla 6–8 mm. wide when expanded.

ECUADOR: 'Andes,' alt. 3300 m., *Jameson 364* (G). Loja, alt. 2800 m., *Jameson 91* (K); *Hartweg 746* (B, K).

PERU: Piura: Ayavaca, *Humboldt & Bonpland* (B, type fragment); *Weberbauer 6387* (F, N). Ayacucho: Between Tambo and Río Apurimac, 3200 m., *Weberbauer 5589* (F).

BOLIVIA: without locality: *Bang 1885* (B, F, G, N, Y). Cochabamba: Incachaca, alt. 2300 m., *Steinbach 8863* (B), 9204 (B). Cochabamba, *Bang 1087* (A, F, G, N, Y). La Paz: Unduavi, alt. 3100 m., *Buchtien 3005* (N, Y); *Rusby 725* (B, F, G, N, Y).

This is one of the earlier described species to which many specimens have been referred. Those listed above are the only ones which we consider true *V. ayavacense*. We have not seen the type of *V. Witteanum* (*Weberbauer 4960*, from Cuzco, Peru), and we refer the species to *V. ayavacense* with doubt. The leaves of the specimens cited above are often much smaller than those described by Graebner, and the corymbs of our specimens never approach the maximum given in the original description of *V. Witteanum*.

21. VIBURNUM TORONIS Killip & Smith, Bull. Torrey Club **56**: 274. 1929.

COLOMBIA: Antioquia: *Toro 424* (Y, type, N).

22. VIBURNUM CORNIFOLIUM Killip & Smith, Bull. Torrey Club **56**: 273. 1929.

COLOMBIA: Antioquia: *Toro 1377* (Y). El Valle: *Killip 11648* (N, type, G, Y), *11206* (G, N, Y).

23. VIBURNUM RORAIMENSE Killip & Smith, Bull. Torrey Club **56**: 406. 1929.

BRITISH GUIANA: Mt. Roraima: *Tate 509* (Y, type)[1]; *Im Thurn 220* (N).

24. VIBURNUM DIVARICATUM Benth. Pl. Hartw. 132. 1844. *Oreinotinus divaricatus* Oerst. Kjoeb. Vid. Medd. **1860**: 287. 1861.

ECUADOR: 'Mountains of Paccha,' *Hartweg 747* (K, type).

25. VIBURNUM LEHMANNII Killip & Smith, Bull. Torrey Club **56**: 274. 1929.

COLOMBIA: El Cauca: *Lehmann BT671* (Y, type, N), *969* (Y).

26. **Viburnum antioquiense** sp. nov. Tree about 6 m. high; branchlets minutely and sparingly stellate-pubescent, at length glabrous; petioles 6–10 mm. long, stellate-pubescent; leaves elliptic to oblong, 7–13 cm. long, 3–6 cm. wide, triangular-acuminate at apex, cuneate or subrotund at base, coarsely crenate-dentate to base (teeth callose-thickened, about 1 cm. apart, each terminating a veinlet), glabrous, minutely stellate-tomentose on midnerve above, softly stellate-pilosulous on midnerve beneath and in axils, the veins 5 to a side, ascending; peduncles 4.5–7 cm. long, densely stellate-tomentellous; corymbs 5–10 cm. wide at anthesis, 7-rayed (primary rays 2–4 cm. long), 3- or 4-times branched, pubescent as the peduncle, bracteolate, the bractlets linear, about 2 mm. long; calyx tube turbinate, glabrous, eglandular, the lobes orbicular-ovate, 0.5 mm. long; corolla 3–4 mm. wide when expanded, the lobes orbicular-ovate, minutely crenulate.

Type, *Archer 568*, collected August 31, 1930, at Cafetal La Suiza, Titiribí, dept. Antioquia, Colombia, alt. 1700 m., and deposited in the U. S. National Herbarium (no. 1,444,992). Duplicate Y.

27. **Viburnum subsessile** sp. nov. Tree 4–6 m. high, the branchlets densely stellate-tomentose, at length glabrous; petioles up to 3 mm. long, glabrous or sparingly stellate-hirsutulous; leaves ovate-oblong, 5–8 cm. long, 2.5–4.5 cm. wide, obtuse at apex, rounded at base, coriaceous, glabrous or occasionally tomentulose in axils of nerves beneath, nerves strongly elevated beneath, the principal lateral nerves 3 or 4 to a side, ascending; peduncles 4–5 cm. long, stellate-tomentose; corymbs 4–5.5 cm. wide, 5–8-rayed (primary rays 1–1.5 cm. long, stellate-tomentose), 3-times branched, bracteolate, the bractlets narrowly linear, up to 2 mm. long; calyx tube about 1 mm. long, glabrous, eglandular, the lobes triangular-ovate, 0.8 mm. long, subacute; corolla 3–4 mm. wide when expanded, the lobes orbicular-oblong; fruit 'a small black berry.'

[1] In the original publication the type was erroneously cited as *Tate 500*.

Type, *Kalbreyer 533*, collected on open mountain slopes, Jan. 14, 1878, at Ocaña, dept. Norte de Santander, Colombia, alt. about 1800 m., and deposited in the herbarium of the Royal Botanic Gardens, Kew. Duplicate B. This species is at once distinguished from near relatives by the subsessile obtuse leaves.

28. VIBURNUM JELSKII Zahlbr. Annal. Naturk. Hofmus. Wien **7**: 1. 1892. Small tree; branchlets densely rufo-stellate-tomentose, at length glabrous; leaves ovate or oblong-ovate, 6–12 cm. long, 4–7 cm. wide, acuminate at apex, rounded or subacute at base, callose-dentate or subentire, essentially glabrous, stellate-pubescent on nerves and in axils beneath, subcoriaceous, the nerves 4 or 5 to a side; corymbs 6–10 cm. wide, finely stellate-tomentose at anthesis, 6- or 7-rayed, the rays 2–4 cm. long; calyx tube 1–1.5 mm. long, glabrous, the lobes triangular-oblong; corolla about 4 mm. wide when expanded; fruit ovoid, up to 10 mm. long and 6 mm. in diameter.

Type locality: near Cutervo, Dept. Cajamarca, Peru (*Jelski 35*).

ECUADOR: Loja: Loja, *Seemann 8531* (K).

PERU: Amazonas: Panahuanca, *Mathews 1198* (K). San Martín: Tarapoto, *Spruce 4835* (K); San Roque, alt. 1400 m., *L. Williams 6997* (N), *7170* (N), *7495* (N), *7779* (N). Ayacucho: Ccarrapa, alt. 1000 m., *Killip & Smith 22409* (N, Y), *22496* (N, Y), *22498* (N, Y). Aina, alt. 900 m., *Killip & Smith 22734* (N, Y), *23128* (N, Y), *23132* (N, Y), *23172* (N, Y). Cuzco: Urubamba Valley, alt. 1800 m., *Cook & Gilbert 1157* (N).

'CHILI:' *Poeppig 1309* (B).

There seem to be no important differences between the specimens from south-central Peru and those from the northern departments. The indument of all of these specimens is much denser than indicated in the original description, but, as Zahlbruckner notes, the type specimen was well past anthesis.

29. VIBURNUM SEEMENII Graebn. Bot. Jahrb. **37**: 435. 1906. Much-branched shrub, the branches divergent, elongate, finely stellate-tomentellous, at length glabrous; leaves ovate or ovate-oblong, 5–12 cm. long, 2–7 cm. wide, acuminate or triangular-acuminate at apex, subrotund or cuneate at base, dentate in upper half or entire, glabrous above, sparingly pubescent beneath; inflorescence subaxillary as well as terminal, the corymbs borne on numerous short leafy branches, 5–10 cm. wide at anthesis (rarely larger), 5–7-rayed, the rays slender, 2–2.5 cm. long, minutely stellate-tomentellous or glabrescent; corolla 3–4 mm. wide when expanded; fruit ovoid.

The typical form is characterized by a very short tomentum, the hairs not over 0.2 mm. long. It is represented by the following specimens:

BOLIVIA: La Paz: Yungas, *Bang 371* (B, type, F, G, N, Y); *Rusby 2584* (N, Y). Milluguaya, 1300 m., *Buchtien 767* (F, G, K, N, Y). Mapirí, 800–1600 m., *Rusby 2469* (G, N, Y); *Buchtien 1519* (N, Y). Apolo, 1500 m., *R. S. Williams 150* (N, Y), 320 (N, Y). Tipuani, 1400 m., *Buchtien 5601* (N), *7521* (N), *7522* (N).

The following forms may be recognized:

**Viburnum Seemenii f. bolivianum** (Gandoger) comb. nov. *Viburnum bolivianum* Gandoger, Bull. Soc. Bot. France **65**: 33. 1918. Indument softly yellow-tomentose, the hairs 0.3–0.4 mm. long.

PERU: Cuzco: Lucumayo Valley, *Cook & Gilbert 1388* (N). Local name: Pucañahui.

BOLIVIA: without locality, *Bang 2840* (B, F, G, N, Y). La Paz: Yungas, 1200 m., *Bang 370* (type coll. of *V. bolivianum*, F, G, N, Y); Soratá, 3000 m., *Rusby 726* (Y); Guanai, 650 m., *Rusby 2560* (Y); Sirupaya, 2100 m., *Buchtien 250* (N); Coroico, 1100 m., *Buchtien 296* (B, F, G, Y), *5759* (K, N); Milluguaya, 1300 m., *Buchtien 187* (G).

**Viburnum Seemenii f. minus,** f. nov. Leaves 5–7 cm. long, 2–3 cm. wide, entire; branchlets essentially glabrous, the rays sparingly tomentose, the hairs up to 0.3 mm. long; corymbs up to 5 cm. wide at anthesis.

Type, *Steinbach 6063*, collected on Cuesta Negro, Dept. Santa Cruz, Bolivia, alt. 1200 m., Dec. 23, 1921, and deposited in the herbarium of the Field Museum of Natural History (no. 552860). Duplicate B.

BOLIVIA: Cuesta Santa Luisina, *Hieronymus & Lorentz 641* (B). Cuesta del Tambo, *Hieronymus & Lorentz 883* (B). Santa Cruz: Samaipata, 1500 m., *Steinbach 3750* (B). Cuesta Negro, 1200 m., *Steinbach 6066* (B). Cerro Hosana, 1300 m., *Steinbach 3369* (B). Comarapa, 2800 m., *Steinbach 8420* (B, Y).

### DOUBTFUL SPECIES

VIBURNUM RETICULATUM R. & P.; Oerst. Kjoeb. Vid. Medd. **1860**: 286 (err. typ. 386). 1861, as synonym. *Oreinotinus reticulatus* Oerst. Kjoeb. Vid. Medd. **1860**: 286 (err. typ. 386). 1861. Description of fruit only; specimen not seen by us.

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NEW YORK BOTANICAL GARDEN

## INDEX TO AMERICAN BOTANICAL LITERATURE
### 1925–1930

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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**Agrelius, F. U. G.** Botanical notes 1921–1928. Trans. Kansas Acad. Sci. **32**: 117–128. 1929.

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**Alexander, E. J.** *Viola Priceana*. Addisonia **14**: 55–56. *pl. 476*. "D 1929" 28 F 1930.

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**Anderson, H. W.** Experiments with blister canker of apple trees. Univ. Illinois Agr. Exp. Sta. Bull. 340: 55–90. *f. 1–16*. Ja 1930.

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**Andrews, A. L.** Holzinger's No. 663. Bryologist **32**: 109. "N 1929" 11 Mr 1930.

*Pohlia proligera.*

**Ansembourg, V. d'.** Notes sur la flore et la faune de l'Uruguay. Bol. Mensuels Monats. **22**: 56–60; 61–80. 1929.

**Arnold, C. A.** The genus *Callixylon* from the Upper Devonian of central and western New York. Papers Michigan Acad. Sci. 11: 1–50. *pl. 1–19*. F 1930.

**Arny, A. C., & others.** Reed canary grass. Minnesota Agr. Exp. Sta. Bull. 252: 1–19. *f. 1–6*. Mr 1929.

**Avery, G. S. Jr.** Comparative anatomy and morphology of

embryos and seedlings of maize, oats, and wheat. Bot. Gaz. **89**: 1–39. *f. 1–68.* 20 Mr 1930.

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**Beadle, G. W.** Heritable characters in maize. XXXIII. Slit leaf blade. Jour. Heredity **21**: 45–48. *f. 26–28.* Ja 1930.

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**Billington, C.** The flora of two acres of farm land in Oakland County, Michigan. Papers Michigan Acad. Sci. **11**: 51–73. *pl.* 20. F 1930.

**Bishop, H.** The Austin collection from the Labrador coast. Rhodora **32**: 59–62. 8 Mr 1930.

**Blagg, B.** Moss notes from Cold Spring Harbor, Long Island, N. Y., July, 1929. Bryologist **32**: 107. *pl. 6.* "N 1929" 11 Mr 1930.

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**Blinks, L. R.** Comparison of resistance changes in collodion membranes and cells. Proc. Soc. Exp. Biol. & Med. **26**: 359–360. 1929.

**Blinks, L. R.** The direct current resistance of *Nitella*. Jour. Gen. Physiol. **13**: 495–508. *pl. 6, 7+f. 1, 2.* 20 Mr 1930.

**Blinks, L. R., Harris, E. S., & Osterhout, W. J. V.** Studies on stimulation in *Nitella*. Proc. Soc. Exp. Biol. & Med. **26**: 836–838. 1929.

**Bödecker, F.** *Coryphantha Mühlbaueriana* Böd. spec. nov. Monats. Deutsch. Kakteen-Gesell. **2**: 18–20. *illust.* Ja 1930.

**Bödecker, F.** *Coryphantha obscura* Böd. sp. n. Monats. Deutsch. Kakteen-Gesell. **2**: 25–26. *illust.* F 1930.

A Mexican plant.

**Bödecker, F.** *Coryphantha speciosa* Böd. spec. nova. Monats. Deutsch. Kakteen-Gessell. **2**: 23–24. *illust.* F 1930.

A plant from Mexico.

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**Branstetter, B. B.** Corn root rot studies. Missouri Agr. Exp. Sta. Res. Bull. 113: 1–80. *pl. 1–8+f. 1–5.* N 1927.

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# The chloroplasts of Selaginella

ROBERTA MOHLING MA

(WITH PLATE 10)

The writer, in an earlier paper (Ma, 1928) has described the contents of the plastids of the cells of the young leaves of *Isoetes melanopoda*. These plastids contain blue-staining starch grains and red-staining granules (when the Flemming triple stain is used) which are considered to be similar to the pyrenoid-bodies of the spore mother cells of *Anthoceros* and *Notothylas* as described by McAllister (1927). The single plastid in a cell of the young leaf of *Isoetes melanopoda* shows numerous starch grains and red-staining granules. While the older cells of the leaf may contain as many as thirty plastids, they are proportionately smaller and, of necessity, contain fewer starch grains and red-staining granules.

Marquette (1907, 1908) has described red- and violet-staining bodies in 'polar structures' in cells of young leaves of *Isoetes lacustris*, and in the pollen mother cells of *Marsilia quadrifolia*. Though he does not call these 'polar structures' plastids he points out the resemblance between these and the bodies in the chromatophores of *Anthoceros*. Marquette states (1907): 'It is highly desirable that a re-investigation of the spore-mother cells as well as the vegetative cells of *Anthoceros* and likewise the epidermal assimilatory cells of *Selaginella* be undertaken from this standpoint.'

The writer has shown that in *Isoetes melanopoda* similar well-defined structures, usually occupying a polar position, divide to form the numerous plastids of the older cells (Ma, 1928).

McAllister (1914) has shown that the single chloroplast of the cells of the active gametophyte of *Anthoceros* contains an aggregation of spindle-shaped bodies which he calls pyrenoid bodies. These bodies occupy the central region of a plastid and they are usually surrounded by starch grains of the same shape as that of the pyrenoid bodies. He concludes, after comparing the size and shape of the starch grains with the pyrenoid bodies, that the starch grains are derived from pyrenoid bodies.

Haberlandt (1888, 1905) has investigated the chloroplasts of the epidermal assimilatory cells of the foliage leaves of several species of *Selaginella*. He found that each young cell of the leaves of *S. Martensii* usually contains a single, large, bowl-shaped chloroplast. These plastids commonly contain numerous starch grains which tend to be more or less grouped in the center of the plastids.

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Bei geringerem Stärkereichthum waren die Stärkekörnchen nicht gleichmässig im Chloroplasten vertheilt, sie traten vielmehr dicht gedrängt in der Nähe des dem Chlorophyll-körper angelagerten Zellkerns auf, während die übrigen Theile des Chloroplasten vollständig stärkefrei waren.

The writer has studied the chloroplasts of the cells of the assimilative leaves of *Selaginella apus* (L.) Spring, *Selaginella Riddellii* Van Essel., and *Selaginella Wrightii* Hieron. Special attention has been given to the blue-staining starch grains and the safranin-staining bodies found in these plastids, with emphasis on the origin, and subsequent development of the red-staining bodies.

## MATERIALS AND METHODS

*Selaginella apus*, though widely distributed in protected places, is not abundant in central Texas. *Selaginella Riddellii* is the common *rupestris* type of the region, while *Selaginella Wrightii* appears to be more restricted to the western half of the state.

Merkel's fluid and weak chromic acetic acid were used as fixing media. For the purpose of studying the cell contents or the contents of plastids, Merkel's fixing solution proved to be most satisfactory.

Since Flemming's triple stain is especially favorable in the differentiation of starch grains and pyrenoid-bodies (McAllister,1914, 1927), it has been used chiefly in the present investigation of *Selaginella*. With this stain the starch grains take on a blue color, the pyrenoid-like bodies a red color, and the cytoplasm a yellowish color. Since with an excess of violet stain both starch grains and pyrenoid-bodies stain violet, Haidenhain's iron-alum haematoxylin has been used to check the red-staining bodies. In this stain the red bodies stain dark gray or black, while the starch grains are colorless. Iodine gives the characteristic starch reaction with the bodies which take the violet of triple stain, but has no effect on the red-staining bodies. Millon's reagent has been employed to demonstrate the protein nature of the red-staining bodies.

## OBSERVATIONS

The cells of the young leaves have been investigated in three species of *Selaginella: S. Riddellii*, *S. Wrightii*, and *S. apus*. In the leaves of *S. Riddellii* and of *S. Wrightii* there are at least four and often as many as sixteen plastids in each cell. The plastids are either oblong or crescent-shaped. They measure 1.4 to 2.0 microns in width and 2.3 to 5.0 microns in length. In these small plastids, it is difficult to distinguish clearly the contents even though the highest magnification be used. Therefore the observations of the present study have been based for the most part upon the cells of

the leaves of *S. apus*, in which a single plastid is found in most cells.

The leaves of *S. apus* are made up of two to three layers of cells: fairly well-defined upper and lower epidermal layers, and the spongy internal layer, one cell in thickness at the margins and tip of the leaf, and two cells in thickness in the middle regions and base of the leaf. The cells of the upper layer of the leaf are thimble- or bowl-shaped, with the smaller end to the interior (figs. 2, 4). The cells of the spongy layer are irregular in shape with large, irregular, intercellular spaces between them (figs. 5, 7). The cells of the lower layer of the leaf are rectangular in outline (figs. 14, 16).

The shape and size of the plastid vary with the position of the cell. The cells of the upper layer contain a single thick-walled, bowl-shaped plastid, with the nucleus in the cavity of the bowl (figs. 1, 2, 3). In *S. Martensii*, Haberlandt (1888, 1905) has described a similar plastid as 'ein grosser muldenförmiger Chlorophyllkörper.' From their contents, size, and position in the leaf, it is apparent that the plastids of the upper layer of cells are far the most important in photosynthesis. In the cells of the spongy layer and the lower epidermis of the leaf, the plastids are oblong-ellipsoid or crescent-shaped, and are considerably smaller than those seen in the upper layer. These plastids measure from 6.5 to 18.0 microns in their longest and 2.6 to 7.0 microns in their shortest dimension.

As has been stated above, the cells of young leaves usually contain a single, large plastid (figs. 3, 5), though sometimes there are two plastids to a cell (figs. 4, 9, 17). However, in a single leaf the number of plastids often varies from one to four: the cells of the upper external layer of cells contain one to two plastids, those of the middle or the spongy layer and the lower layer of cells one to four plastids. It is also observed that the cells near the tip of a leaf contain usually one plastid and the cells near the base of a leaf two or more plastids.

The plastids of the cells of the growing point and leaf-rudiment contain definite rounded granules of varying size, but, due to their minuteness, their staining reaction cannot be definitely determined (figs. 1, 2, 3, 13, 14). By the time the leaves have reached a length of 0.2 mm., spindle-shaped red-staining bodies are clearly recognizable in the plastids (figs. 5, 10, 18). The number cannot be determined with certainty, for, though the largest are easily recognized, smaller bodies are present which seem quite similar to the larger ones, the staining reaction of which is not clear. As the plastids enlarge with the increase in size of the cells, the red-staining bodies also increase in size. There is also an apparent increase in number in these bodies, but, since it is difficult to be certain of the number of the younger cells, the increase in number may be due to the greater definiteness in these older cells.

In the older leaves of *S. apus* the plastids contain from two to twenty minute bodies, which are usually elongated, spindle-shaped, and varying in length from 0.5 to 2.0 microns (figs. 6, 12). In some plastids all of these bodies stain red with the safranin of Flemming's triple stain (fig. 12); in other plastids some of the bodies stain red and some stain blue in the triple stain (figs. 8, 10). In still other plastids all of the bodies stain blue (figs. 9, 11). In cells of leaves close to the growing point usually only red-staining bodies are present (figs. 7, 12). In the cells of mature leaves, the blue-staining bodies predominate (figs. 6, 8, 9).

In plastids containing both red- and blue-staining bodies, there seems to be no constant difference in the size of the two kinds of bodies (figs. 4, 8). They are, in most cases, collected in a loose aggregation near the center of the plastid, often leaving a free zone at the periphery (fig. 12). Frequently plastids may be seen in which the red-staining bodies occupy the center and are surrounded by the blue bodies (fig. 8). In other plastids the two kinds of bodies are mixed together (fig. 17). In such plastids the red- and blue-staining bodies are the same shape and size, and have the same orientation in the plastids. The only visible difference between the two kinds of bodies when stained with the Flemming's triple stain is the color-reaction.

Occasionally, cells show plastids containing blue starch grains, and also bodies of similar shape and size, whose stain-reaction is not quite violet and yet not red. These bodies are often surrounded by starch grains (fig. 18), though in some cases they may be located at one side of the plastid (fig. 17). They are also found surrounding red-staining bodies in a plastid (fig. 7). The plastids containing these bodies are often to be found adjacent to plastids containing all red-staining bodies (fig. 10), indicating that the violet stain is not in excess. The reddish-blue bodies, therefore, can not be imperfectly stained red bodies containing an excess of violet stain. This intermediate staining reaction may indicate a transition of the red-colored bodies through reddish purple to the typical blue or violet color of starch grains. In cells of a given region, the red- and blue-stained bodies are similar in size and shape, whether they are all red-stained or all blue-stained, or part red and part blue. As has been stated above, they differ visibly only in their staining reaction. It is difficult to conceive how bodies so similar in shape and size could exist mixed together in the same plastid, without there being a close relationship between them.

When treated with Millon's reagent, the red bodies in the plastids of the cells of *S. apus* gave a positive protein reaction. Neighboring sections of a young tip of *S. apus* were stained with Flemming's triple stain and Millon's reagent. The same areas which contained an excess of bodies

stained red with Flemming's triple stain also contained an excess of bodies stained reddish with Millon's reagent. These bodies in the plastids of *S. apus* are similar chemically to the pyrenoid-bodies in *Anthoceros* and *Notothylas* (McAllister, 1914, 1927), and also similar in this respect to the pyrenoids of *Hydrodictyon utriculatum*, as reported by Timberlake (1901). This chemical similarity, together with the similarity in shape and the relation to the starch grains, suggests very strongly that the red-staining bodies in the plastids of *Selaginella* are similar in function to the pyrenoid bodies of *Anthoceros*.

In the mature leaves the plastids usually contain blue-staining starch grains alone (figs. 6, 11). These starch grains are slightly larger than the rudimentary starch grains, though there is no such conspicuous enlargement as in the case of rudimentary starch grains of *Anthoceros* or of *Isoetes*. Sometimes these mature grains are rounded off at the ends, changing from spindle-shaped to egg-shaped starch grains (figs. 15, 16). This difference in shape is probably due to the partial solution by enzymes.

## DISCUSSION AND SUMMARY

According to the observations above, the number of plastids of the cells of the leaves of different species of *Selaginella* varies considerably. The cells of the leaves of *S. Riddellii* and of *S. Wrightii* usually contain from four to sixteen plastids. In the cells of the leaves of *S. apus*, on the other hand, the plastids are few in number and proportionately larger. The contents of these larger plastids are naturally more conspicuous than those in the small plastids. The plastids contain spindle-shaped red- and blue-staining bodies. The red-staining bodies react positively to Millon's reagent for protein, and the blue-staining bodies are found to be starch when tested with iodine. Four to twenty of these bodies make up a loose aggregation in the central region of the plastids. There is no constant difference in the size or in the shape of these protein and starch bodies. They differ visibly only in their staining reaction.

From the close similarity of these two kinds of bodies in size and shape, it seems probable that there must be some close relationship existing between them. It is quite likely that one arises from the other. That starch is formed as a transformation of the protein bodies is strongly suggested by the gradual disappearance of the protein bodies as starch grains become more abundant. In regions where growth is active and where demands for carbohydrates are correspondingly great, very little starch is present, while the red-staining bodies are common. In mature cells favorably located for photosynthesis, starch grains are in excess and the red bodies are practically lacking. The writer has also called attention to what

seem to be transitional stages from the protein bodies to starch grains; these bodies having a stain intermediate between red and blue are found with bodies staining distinctly red or blue. From the evidence given above it seems reasonable to conclude that the red-staining bodies of *S. apus* give rise to rudimentary starch grains.

In the single large plastid of the thallus of *Anthoceros*, McAllister (1914) has described safranin-staining bodies, which he has called 'pyrenoid-bodies,' and violet-staining starch grains. These pyrenoid-bodies are similar in shape, color-reaction, and protein-test to those red-staining bodies found in the single large plastids of S. *apus* as described in the present investigation. In the plastids of *Isoetes* (Ma, 1928) there are red-staining granules mingled with the blue-staining starch grains. These granules are not similar in shape to the red-staining bodies of *S. apus*, but in shape and color-reaction they are similar to the pyrenoid-bodies of the spore mother cells of *Anthoceros* and *Notothylas*. McAllister concludes that the pyrenoid-bodies of *Anthoceros* and *Notothylas* give rise to rudimentary starch grains.

Marquette (1907, 1908) has described small red-staining granules lying among the starch grains in the 'polar structures' of cells of young leaves of *Isoetes lacustris* and also in spore mother cells of *Equisetum* and *Marsilia quadrifolia*. The writer has observed such bodies in the single plastids of the sporogenous cells of various mosses, and it is probable that such bodies are present in all single, large plastids. Whenever the staining reaction of the contents is distinct, these red-staining bodies are present either by themselves, or mixed with starch grains. These red-staining bodies, however, may be present even in the smallest plastids, though sometimes they may be too minute to be recognized with certainty through the color-reaction. For instance, in the cells of the leaves of *Isoetes melanopoda* (Ma, 1928) the number of plastids varies in different cells, and the number of red- and violet-staining bodies of each individual plastid is also variable. As the number of plastids to each cell is increased, these bodies are reduced somewhat both in number and in size, so that the number of plastids to a cell ranges from one to thirty, and the number of the red- and violet-staining bodies to each plastid probably from seven to thirty. When plastids are numerous in the cell their size is naturally smaller. Minute bodies are present in these small plastids, the color reaction of which is only occasionally distinguishable. Since in larger plastids minute starch grains and red-staining protein bodies are both present, these minute bodies in the small plastids may be rudimentary red-staining bodies and starch grains. It seems reasonable to expect that if a definite relation exists between the starch grains and the red-staining protein bodies in the larger

plastids, a similar relation also exists between corresponding bodies in the smaller plastids.

This work has been done in the botanical laboratories of the University of Texas, and the writer wishes to express her appreciation to Professor Frederick McAllister, who suggested the problem and has given invaluable assistance and encouragement.

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## Explanation of plate 10

Drawings were made with the aid of the camera lucida, with the microscope elevated to increase the magnification. All figures were taken from the cells of the young leaves of *Selaginella apus* (L.) Spring. The original magnification was approximately 2,300 diameters, but this has been reduced in reproduction to about 1530 diameters.

Fig. 1. Cell taken from the upper layer of the innermost rudimentary leaf, showing bowl-shaped plastid.

Figs. 2, 3. Cell taken from the upper layer of the third leaf. Plastid shows granules, the staining-reaction of which is not clear.

Fig. 4. Cell taken from the upper layer of an older leaf showing two plastids, with blue-staining starch grains surrounding a red-staining body, and between them intermediate, reddish-blue-staining bodies.

Fig. 5. Cells from spongy layer each showing single plastid; one contains a plastid with spindle-shaped red-staining bodies, and the other blue-staining starch grains.

Fig. 6. Cell of spongy layer showing plastids containing spindle-shaped starch grains.

Fig. 7. Cell similar to the one above, showing two plastids; one contains red-staining bodies and the other a red-staining body surrounded by reddish-blue bodies.

Fig. 8. Cell taken from spongy layer, showing two plastids; one containing red and blue bodies and the other blue-staining starch grains.

Fig. 9. Cell of the spongy layer showing plastid division and plastids containing blue starch grains.

Fig. 10. Cell of the spongy layer near the base of a leaf showing three plastids, two of which contain red-staining bodies only, the third red-staining bodies and bodies staining reddish-blue.

Fig. 11. Cell of spongy layer near the base of a leaf showing three plastids containing starch grains.

Fig. 12. Cell from the spongy layer near the base of a leaf showing plastids with red-staining bodies.

Fig. 13. Cell taken from the upper layer of a leaf rudiment showing a single plastid with indistinct contents.

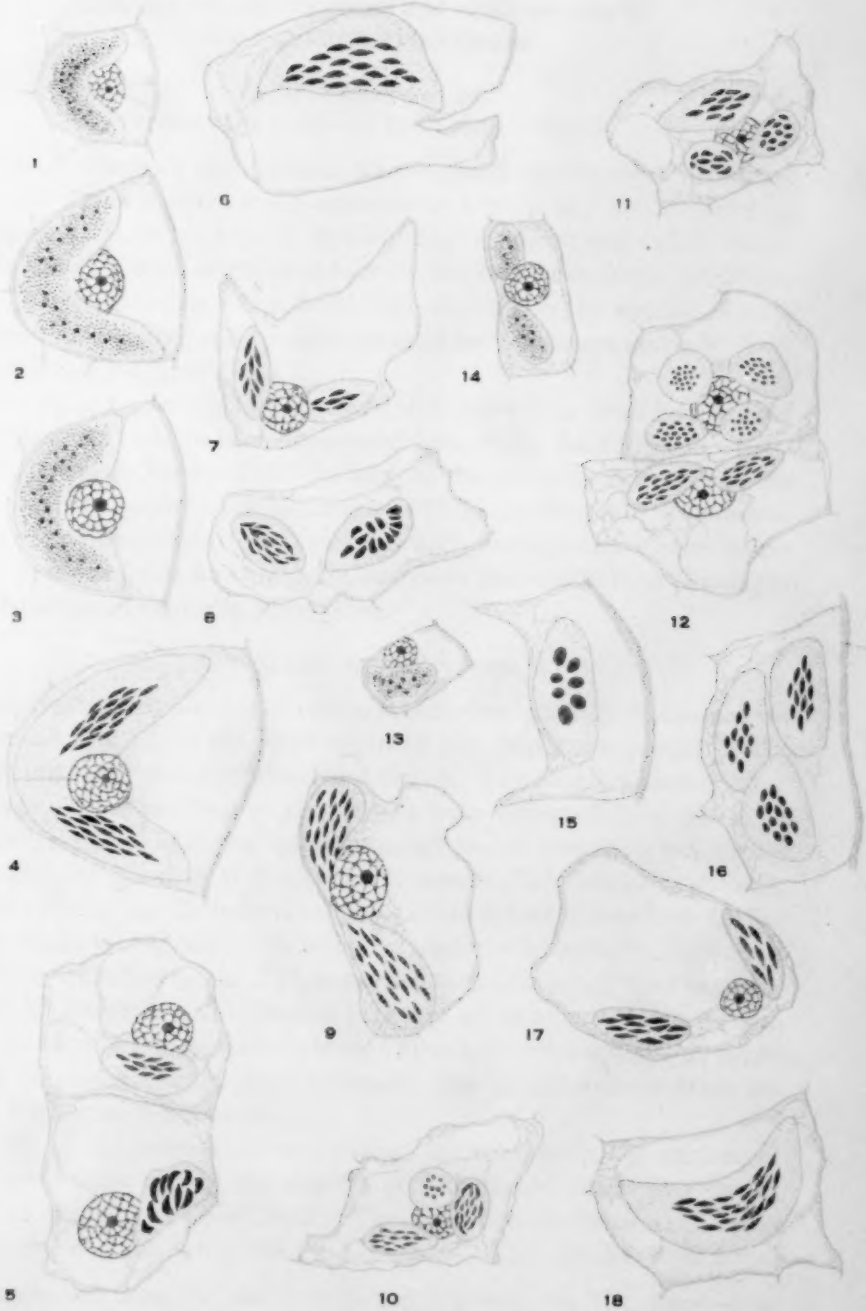
Fig. 14. Cell from the lower layer of first leaf showing two plastids. Indefinite bodies present.

Fig. 15. Cell taken from the lower layer of an older leaf showing one plastid.

Fig. 16. Cell of the lower layer near the base of a leaf showing three plastids, containing starch grains.

Fig. 17. Cell of the spongy layer showing two plastids containing starch gains and at one end bodies with staining-reaction intermediate between red and blue.

Fig. 18. Cell of spongy layer, showing bodies with staining-reaction intermediate between red and blue, surrounded by starch grains.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# The development of pollen and viscin strands in Rhododendron catawbiense[1]

CLEMENT GRAY BOWERS
(WITH PLATES 11–15 AND THREE TEXT FIGURES)

In Rhododendrons and Azaleas, together with certain other ericaceous plants, the pollen grains remain adherent in tetrads and are provided on their outer surfaces with long, hyaline fibrils, sometimes called 'viscin threads.' Each tetrad, or group of four microspores, is enclosed within one common outer covering. The thread-like strands on the outside of each tetrad serve to connect and to entangle neighboring groups and hold them together in loose aggregations.

These facts regarding the viscin strands have long been known, but nothing appears to have been discovered concerning their origin and nature, and little was known of the cytology of the pollen mother-cells of the heaths until the recent work of Longley (1927) on the genus *Vaccinium*.

I have studied especially the origin and development of the viscin strands in *Rhododendron catawbiense*, and have also worked out the stages in the reduction divisions in this species.

## MATERIALS AND METHODS

*Rhododendron catawbiense* Michaux was chosen for study, because of its wide availability. It is the most common and important parent of the horticultural races now cultivated in America. The plants I have studied are presumably of seedling origin, having been collected from the wild. They are quite typical of the species, mature plants averaging five feet in height, and are growing at the Hicks Nurseries, Westbury, New York. Material taken from six individual plants was found to be quite similar when studied cytologically. Three clonal varieties of hybrid origin were also used to a limited extent. These are the varieties named 'Atrosanguineum,' 'H. W. Sargent,' and 'Ignatius Sargent,' all members of the cultigen group known as '*R. catawbiense* hybrids.' Four additional species, *R. maximum*, *R. carolinianum*, *R. calendulaceum*, and *R. arborescens* were examined for chromosome numbers.

Meiosis in rhododendrons and azaleas takes place in the anthers of young flower buds during the months of August and September in the vicinity of the city of New York. The reduction divisions thus occur seven to nine months before the flowers bloom. This fact has been noted

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by Samuelsson (1913) and others as true for various genera in the Ericaceae. In *Rhododendron catawbiense*, heterotypic division occurs about the first week in September. It has been found to vary to the extent of a week or ten days, depending upon location and season.

All the phases of microspore formation here reported for *R. catawbiense* were studied from material imbedded in paraffin and sectioned by the usual cytological methods. As a fixing solution, Flemming's fluid, medium strength, was found to be generally as satisfactory as any of the others tried, although for the late stages following the thickening of the pollen walls, Flemming's strong solution seemed preferable. Other fixing agents employed were chrom-acetic acid, Bouin's solution, Němec's solution, and Allen's solution.

For staining the imbedded and sectioned pollen mother-cells, Flemming's triple stain (safranin, gentian violet, and orange G) was used effectively at all stages of meiosis, but Delafield's haematoxylin, used after iron-alum, was found to be particularly desirable for the study of chromosomes, spindle fibers, and the early stages of viscin strand formation. According to this method, the sections are first treated for 30 minutes in 4 per cent iron-alum, then rinsed in water and immersed in Delafield's haematoxylin solution for from three to five minutes. They are then carried through the alcohol series, being destained to the proper density when 50 per cent alcohol is reached by the addition to this solution of about 3 per cent concentrated hydrochloric acid. Later they are counter-stained with orange G (1 per cent added to clove oil). Heidenhain's haematoxylin was also employed.

For staining the middle lamella and the earliest stage of viscin strand formation, ruthenium red was particularly useful. This stain in aqueous solution, 1 to 5,000, as employed by Mangin (1893) and Allen (1901), gave good results both with and without the addition of 1 per cent concentrated ammonium hydrate. The material was immersed in the staining solution for one hour, then rinsed, carried through the alcohol series and mounted in Canada balsam. Although not entirely specific, as Harlow (1928) observed, ruthenium red is, nevertheless, of great value in studying the middle lamella. Orange G was sometimes used effectively in combination with ruthenium red to bring out the special mother-cell walls. The ruthenium red stain employed was the product marketed under that name by the firm of Eimer and Amend of New York.

For staining the mature pollen tetrads and the viscin strands adhering to them, the technique of Wodehouse (1928c) for the study of pollen grain morphology was found most successful. A small amount of pollen is placed on a glass slide and immersed in a drop of absolute alcohol to dissolve its

waxy coating. It is then rinsed with alcohol and the excess drawn off. A few drops of weak aqueous methyl green (0.2 per cent) are placed on the pollen, and the slide is very gently heated over a flame for one or two minutes in order to promote the rapid staining of the surface without staining the contents of the tetrad. The excess stain is then drawn off and the preparation is mounted in glycerine jelly.

When imbedded and sectioned material containing viscin strands is handled, care must be taken in washing and staining lest the delicate fibrils be broken and then washed off the slide. The strands often do not become readily attached to the slide and many are cut into very small segments during sectioning.

## MORPHOLOGY OF THE MATURE POLLEN

The mature pollen tetrad of *Rhododendron catawbiense* is, as noted, composed of four microspores which are joined together firmly and enclosed in one common outer covering, the four components disposing themselves in a tetrahedral arrangement. The tetrad, therefore, approximates the figure of a tetrahedron with rounded corners (text fig. 25). There is a slight constriction along the lines of contact between the adjoining members of the tetrad, making the structure appear somewhat three-lobed when seen in outline (fig.26). In size, the pollen tetrad is about 45 microns across its broadest diameter.

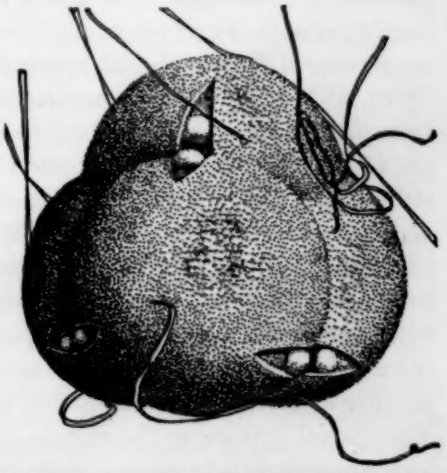


Fig. 25. A mature pollen tetrad with viscin strands adhering to its surface. ×1125.

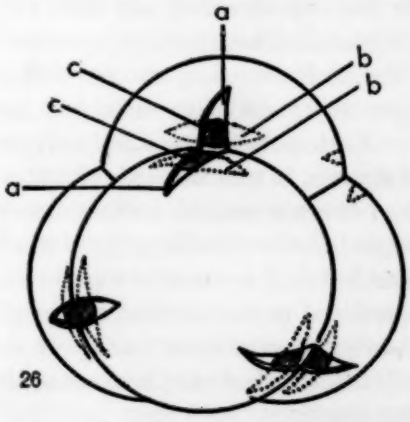
The surface of the exine is of a somewhat granular nature, though this is not especially noticeable on the periphery of the pollen grain when viewed in profile. The surface is covered with an exceedingly thin film of a colorless, waxy substance which is readily soluble in absolute alcohol. This waxy material collects in droplets on a glass slide around the bases of the pollen tetrads after they have been treated with alcohol and the latter has been allowed to evaporate.

There are six long germinal furrows on the outside of each pollen tetrad. Each one of these longitudinal furrows passes, at right angles and at its mid-point, directly across the boundary between adjacent cells of the

tetrad. Each longitudinal furrow is equidistant from its nearest neighbors on either side. The orientation of these furrows is shown in figure 25. The longitudinal furrows are comparatively shallow incisions, cutting through only the outer layer of the exine. The latter is sufficiently transparent to reveal shorter transverse furrows beneath the surface which cut through the inner layers of the exine and cross the longitudinal furrows at right angles (fig. 26), as described for *Mutisia viciaefolia* by Wodehouse (1928b). An opening through the entire wall of the exine is produced wherever a transverse furrow crosses beneath a longitudinal furrow. At such points the inner membrane, or intine, is exposed and protrudes slightly. These openings are the germinal apertures through which the pollen tubes may later emerge. Two transverse furrows cross each longitudinal furrow, one on each of the adjacent microspores, and hence there are two germinal apertures arising out of each longitudinal furrow. With six longitudinal furrows, it will be seen that a complete pollen tetrad carries a complement of twelve germinal apertures, three of which come from each microspore. This is consistent with the number found in many simple pollen grains, where the occurrence of three germinal apertures is relatively common. Wodehouse (1926, 1928 a,b,c) figures numerous simple pollen grains bearing three furrows, each furrow equidistant from the others, along the equator of the grain. Taking one individual microspore of a *Rhododendron* tetrad, as, for example, the foremost member of the pollen tetrad shown in figure 25, and comparing it with the figure of Wodehouse (1928c, pl. 20, fig. 9) for the pollen grain of *Tanacetum*, it will be noted that the orientation of the furrows is exactly the same in both cases. The same comparison may be made with many of the other genera depicted. It may be said, therefore, that the microspores of *R. catawbiense* are very similar to those of certain other families with respect to the number and position of their germinal furrows. The special feature in the case of *Rhododendron* is that the microspores here are united into groups of fours and that the transverse furrows of adjoining microspores develop directly across from one another on opposite sides of a dividing wall, with a single longitudinal furrow passing over both transverse furrows. Two germinal apertures, instead of one, thus arise from one longitudinal furrow. The furrows are somewhat thickened around their margins.

In size, the longitudinal furrows of *Rhododendron catawbiense* pollen average 17 microns long and 3.5 microns wide when opened as in glycerine mounts. The transverse furrows are 9 microns long and about 2.5 microns wide. In germination tests on artificial media, as well as in observations of natural germination on receptive stigmas, it is noticeable that ordinarily only one or two pollen tubes arise from the pollen tetrad. As many as four

tubes have been seen, however, but not commonly. Two or three appear more frequently than four. It is uncommon, also, to see more than one pollen tube emerging from a single longitudinal furrow. Microscopical evidence indicates that the pollen tube enlarges in diameter appreciably soon after it emerges from the germinal aperture, although the pollen tetrad itself does not enlarge at the time of germination. It is conceivable that the pushing forth and enlargement of one pollen tube might so fill the furrow through which it proceeds that germination through the opposite aperture of the same longitudinal furrow would be inhibited through crowding, unless both members of the pair started to send out their tubes simultaneously. The possibility that one germinating microspore may monopolize the moisture or food solutions of the entire tetrad through semi-permeable walls is probably hardly to be considered. There is the further probability that only a part of the surface of the pollen tetrad will come into sufficient



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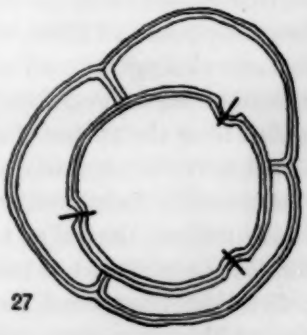
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Fig. 26. Diagram illustrating the relative position of the furrows and germinal apertures on the exine. One longitudinal furrow runs between the points *a* and *a*; it passes from one microspore to another contiguous microspore, crossing the partition wall which separates them. The longitudinal furrows penetrate only part way through the exine walls. Beneath the surface are the transverse furrows, *b* and *b*, cutting across and under the longitudinal furrow as indicated by dotted lines. Openings through the entire exine wall are left at the points *c* and *c*, where longitudinal and transverse furrows meet. The points *c* and *c* thus constitute germinal apertures through which the intine protrudes from beneath.

Fig. 27. Outline drawing showing longitudinal furrows as they first appear from polar view of half-ripened pollen tetrad. They are invisible at earlier stages but are now clearly marked by ruthenium red.

contact with the nutrient medium to make germination possible. It is by no means clear what prevents the development of tubes from all four of the microspores of which the tetrad of *Rhododendron* consists.

Attached to and more or less covering the outer surface of the pollen tetrad as it lies in the anther are numerous thin, hyaline fibrils of various lengths. These are the so-called viscin strands. The photomicrographs (figs. 28, 29) show, more accurately than can be described, the manner in which these fibrils connect the pollen tetrads and hold them together in loose masses. The fine, viscin strands, which are actually much more slender than the photographs indicate owing to optical effects, form an intricate, three-dimensional network. One might describe them as a loose reticulum made up of long and very slender fibers running in all directions and forming a maze of loose, fibrillar material resembling a weft of fleece, but unlike fleece, anastomosing to form a continuous network. Such a nebulous mass has height, depth and thickness, so that it is not to be regarded as a simple net or cob-web-like structure extending in only two dimensions. Instead, it is, figuratively speaking, similar to what a honeycomb might be if the walls of its innumerable cells were to become shredded out into very slender and long thread-like fibrils with branches far apart. The maze is further complicated by the fact that the fibrils, crossing one another or breaking here and there, wind around one another with great facility and become entangled in all sorts of ways. Each pollen tetrad is firmly attached to one or several of these slender strands, so that the mass of mature pollen from the anther of a *Rhododendron* flower resembles a three-dimensional weft of irregularly netted and tangled fibrils with the pollen tetrads rather evenly distributed in it. Being thus fastened to strands of a continuous reticulum, the pollen tetrads are connected to one another and single fibrils running between two or more tetrads may readily be traced. If one pollen tetrad be moved, its neighbors will be disturbed also, because of the thread-like connections which hold them together.

The *Rhododendron* anther discharges its pollen through a pore or opening at the apex of each lobe of the anther, this pore developing, according to Artopoeus (1903) and Matthews and Knox (1926), by the breaking down of a certain set of cells. When the anther is mature and the flower is open small wefts of pollen enmeshed in viscin strands extrude through the pores and reach the open air. When caught by the wind, or adhering to the body of an insect, such a weft of pollen is pulled away from the anther, but as it moves it draws upward out of the anther cavity from below more pollen which is a part of the network. In this manner the entire anther-sac can be completely emptied of its pollen, which may all come out at one time in the form of a single, loose, stringy mass of tangled viscin strands with enmeshed pollen tetrads.

The viscin strands or fibrils are very variable in shape. Most often they are ribbon-like and of unequal width, although in some instances

they appear terete. Their average width may be estimated as approximately 0.5 microns. Their length varies also, but it may attain 150 microns or more, and, in cases where several fibrils are wound together, threads of many times this length may be produced. Individual strands may be branched, but such branchings are neither numerous nor close together. The strands are transparent and appear quite colorless. When mature they are non-elastic, although they frequently unwind out of a tangle and thus may be drawn out to a greater length, simulating elasticity. They are relatively strong in proportion to their size, one or two fibrils being able to draw a cluster of fifty or one hundred pollen tetrads over a plane surface without breaking. The mature pollen is not only attached to the viscin strands, but after it has been shed from the anther it becomes enwrapped by them to a greater or less extent, depending upon how much the weft of strands is tangled.

That the pollen tetrads are actually attached to the viscin strands, however, and not merely entangled in them is indicated by experiment. If pollen tetrads of *R. catawbiense* with their adhering fibrils be covered with a drop of absolute alcohol on a glass slide and observed microscopically while the alcohol evaporates, they will be seen to go through floating motions as the quantity of alcohol decreases, changing their positions from time to time. During these movements, the floating tetrads pull one another here and there, in jerky motions by means of their connecting strands. In cases where the strands become unwound and completely disentangled it would seem that they could no longer hold the pollen tetrads. Yet the latter do not wash free, and they may still be drawn from place to place by strands which are seen to be definitely attached to the walls of the exine, although such attachment is not localized in any specific regions so far as can be determined. Further, if aggregations of pollen tetrads with their strands be put into a vial containing a liquid and shaken violently, many of the strands will be broken off. Subjected to continued violent treatment, such as teasing with dissecting needles, more of the strands can be torn off. Even after such treatment, short pieces of viscin strands still remain adherent to the outer surface of the pollen walls by their ends or lying tightly against the surface of the pollen wall.

As noted, there is no positive evidence that these places of attachment are restricted to definite loci on the pollen tetrad, such as the granular protuberances, the canals between these protuberances, the constrictions over the partition walls, or the furrows. None the less, it seems probable that the method by which the attachment of the viscin strands takes place on the surface of the tetrads, and by which the individual tetrads are connected one with another, is consistent and orderly, and definitely connected

with cell wall formation, the growth of the anther and physio-chemical changes occurring at definite stages. The evidence indicates that at an early stage of development, when the mother cells begin to round up and separate, the middle lamella hydrolyzes into a viscous and semi-liquid condition, and then breaks up into a fibrillar network. Enlargement of the anther cavity at this time through growth of the anther tends to stretch this viscous network and its fibrils come to adhere to the pollen tetrads. Later the fibrils solidify into the condition of a gel and become firmly welded, as it were, to the surface of the pollen tetrads at points where the two were in contact when the physio-chemical changes in the fibrils took place.

In order to determine whether or not the fully mature viscin strands were still at all viscous and sticky, pollen tetrads of *Rhododendron catawbiense* were mixed with pollen grains of another genus having no viscin strands. Pollen grains of *Hemerocallis fulva* were chosen for this experiment, because their size and granular surface resembles that of *Rhododendron* tetrads. After a thorough mixing, during which the *Hemerocallis* pollen became generally distributed throughout the sample of *Rhododendron* pollen, an attempt was made to separate the two kinds. Although well entangled by the network of viscin strands, the *Hemerocallis* pollen was readily separated, both by washing out in water and by teasing out with needles while dry, while the *Rhododendron* pollen could not be freed from the viscin strands.

In occasional instances where a viscin strand is attached to the exine at its end, the strand appears slightly enlarged at the point of attachment, the enlargement resembling a small round or oval disc. There seems, however, to be no regularity about the occurrence of these discs.

The viscin strands of *Rhododendron* pollen will not dissolve in water, alcohol, xylol, ether, or in concentrated sulphuric acid after fifteen minutes immersion in the latter. So far as could be detected, the strands are in no way affected by these reagents. Hence, it may be assumed that they are not of the nature of wax, gum or mucilage. Similarly, they give no tests for fatty or oily materials. They do not react to iodine, or to sulphuric acid, or to chloriodide of zinc as cellulose. They do not become yellow or brown as lignin or proteids when treated with iodine. They do, however, stain fairly well in cyanin after treatment with Javelle water, as recommended by Chamberlain (1924) as a test for suberin. Results on mature pollen grains of *R. catawbiense* with various stains and reagents were as follows:

(1) Viscin fibrils stained fairly well:
Methyl green 0.3 per cent heated

Methylene blue 0.1 per cent heated
Javelle water followed by cyanin 1 per cent

(2) Viscin fibrils stained slightly:
Ruthenium red, aqueous 1/5000, one hour or more
Safranin 1 per cent, 24 hours immersion

(3) Viscin fibrils failed to stain, or practically so:

| | |
|---|---|
| Chloriodide of zinc | Aceto-carmine |
| Heidenhain's iron-haematoxylin | Orange G |
| Delafield's haematoxylin | Gentian violet |
| Light green S.F. yellowish | Bismarck brown |
| Sudan III and IV | Congo red |
| Tincture of iodine | Magenta |
| Thionin | Cresyl blue |

When mature pollen tetrads of *Rhododendron catawbiense* are observed in cross-section, slight thickenings of the exine walls may be seen on either side of each germinal furrow (fig. 24). These thickenings are most pronounced around the longitudinal furrows, although they are also present in lesser degree about the transverse furrows. The wall appears abruptly thickened as it approaches the furrow, then the thickening disappears completely in the furrow itself. A thin membrane develops just inside the inner thickening layer of the pollen cell wall and is distinguishable by its strong affinity for ruthenium red. This is the intine. It protudes slightly at the germinal apertures (figs. 24, 25) and stains very conspicuously at these points with ruthenium red, indicating the presence of pectin or pectic compounds, which doubtless serve here to promote rapid swelling at the time of germination.

Taking the various elements of the spore-coat together, it will be seen that the walls of the pollen tetrad of *R. catawbiense* consist of four layers. The innermost layer, which lies nearest the protoplast, is, as noted, the intine. The three layers lying outside of the intine constitute the exine (fig. 24). These layers are: (1) an inner thickening layer, lying close to the intine and continuous except at definite points, where it is drawn away to form transverse furrows; (2) a dark-staining primary layer, outside the inner thickening layer, which stains with ruthenium red in a manner resembling a middle lamella, and which abuts against the similar layer of microspores next to it in the tetrad to form double partition walls; (3) an outer thickening layer around the periphery of the pollen tetrad, similar to the inner thickening layer in composition and continuous except where drawn away to form longitudinal furrows. The exine of mature pollen tetrads is always a rigid wall and does not swell at germination. The intine swells and extends itself to cover the pollen tube at germination, evidently becoming newly formed from additional material as the growth of the pollen tube proceeds. The partition walls, or septa, consist, as

noted, of double primary walls which occupy a middle position between the inner thickening layers of two adjacent members of the tetrad. That this primary layer, in the partition walls only, is of a double nature is shown by the fact that individual microspores, in rare instances, may be separated from other members of the tetrad by the application of unusual pressure.

One of the most complete descriptions of a pollen grain is that given by Beer (1911) for *Ipomoea purpurea*. Compared with that of the *Rhododendron* pollen tetrad, the spore-coat of *Ipomoea* consists of the same number of layers. The intine is somewhat similar in both cases. The innermost layer of the exine of *Ipomoea*, like that of *Rhododendron*, is thick and culticularized. Next is a layer of rodlets with a homogeneous material running between and among them, out of which spines also arise. The rodlets are first formed upon the inner face of a very thin layer which constitutes the primary layer of the exine, and which at maturity forms the third layer, a very delicate, peripheral lamella with open meshes through which the spines protrude. The microspores of *Ipomoea* are simple pollen grains and are not adherent in tetrads. It will be noted that the spore-coats of *Ipomoea* and *Rhododendron*, though vastly dissimilar externally are somewhat alike in their inner layers.

## THE CELL WALLS AND VISCIN STRANDS

At the archesporial stage, a primary wall surrounds the pollen mother-cells as shown in figures 1, 2 and 4. These walls first appear as thin lines bounding the pollen mother-cells and staining uniformly a bright ruby color with ruthenium red, or a dark violet with Flemming's triple stain. No differentiation of middle lamella and wall layers is recognizable in my preparations. As the cells enlarge the walls thicken, but they still continue to stain entirely red or violet as before, and no differentiation can be seen within them. In all the stages of development shown in figures 1, 2 and 4, the archesporial cell walls appear when stained as of one homogeneous substance. The presence of pectic compounds in these walls is indicated by their affinity for ruthenium red, but whether or not this red-staining material consists of a pectic middle lamella with interior cellulose layers is by no means clear from the preparations made. If cellulose layers are present, they are not sufficiently differentiated to be distinguishable with the technique used. Hence, the evidence on this point must be regarded as inconclusive.

Enlargement of the mother-cell proceeds until the open spireme stage is reached (fig. 5), following which there is no further increase in size until after the homoeotypic division. The ruthenium red-staining layer appears

slightly thinner at the open spireme stage than it was at synizesis, but continues to stain red or violet exactly as before, as do the pectic compounds of the middle lamella as described by Mangin (1893) and Allen (1901). It is evident, however, that the middle lamella giving the pectic staining reaction persists through these growth stages of the mother-cell.

At the time of the open spireme stage the familiar zone of homogeneous apparently gelatinous material which stains with orange G is conspicuous just inside the middle lamella. It appears somewhat as if it might have been formed by the hydrolysis of an inner layer of the archesporial cell wall, but I have not been able to trace the stages of its development. It is at first most dense at the angles of the cell and thins out gradually toward the plasma membrane.

This apparently gelatinous zone was noted in pollen mother-cells by Nägeli (1842), who first used the term 'Spezialmutterzell' to describe it. Since then, the name 'special mother-cell wall' has been commonly used by Strasburger (1898) and others, although the terms 'special wall' and 'special membrane' were employed by Fitting (1900), and 'special wall' was later used by Strasburger (1907) and Beer (1911). Its origin has been much discussed. In *Rhododendron catawbiense* the special mother-cell wall is always present in the late heterotypic prophases and it persists until the homoeotypic division is completed. Its usual appearance is that of a thick, gelatinous zone enveloping the protoplast, but seldom in contact with it in fixed material. Its outer surface is regularly in contact with the red-staining middle lamella and is strongly contrasted with it by not staining with ruthenium red. At the cell angles the outer surface of the special mother-cell wall is sometimes slightly drawn away from the middle lamella (fig. 6), but the contact between the two is usually continuous and complete until much later stages. In rare instances, the inner surface of the orange zone is sharply delimited. Usually there is an open, clear space between the inner surface of the orange zone and the plasma membrane, due probably to shrinkage of the latter in fixation.

From the open spireme stage, in which the special mother-cell wall makes its first appearance, there is no change in the character of the middle lamella or of the special wall until the homoeotypic telophases are completed and the four daughter cells have been organized into a tetrad with partition walls and a continuous peripheral membrane.

Figure 16 shows the formation of cell plates following the homoeotypic division. A series of small dots or enlargements on the spindle fibers appear in the equatorial region of each of the six spindles of the tetrad. These dots become confluent and soon a membrane is formed which stains brightly with ruthenium red or densely with gentian violet. These cell plates are

extended inwardly to the center of the tetrad where they join. They also extend outward to the peripheral cell surfaces where they join the plasma membranes and become continuous with a newly formed peripheral layer which appears at or about the same time that the cell plates are forming. Its first appearance is that of a uniform, delicate line of red-staining material just outside the plasma membrane and in contact with it. The cell plates become double by splitting and appear to be densely stained when observed in edge view, while the peripheral layer is single and appears much less dense (fig. 17). At this stage the cytoplasm appears more or less fibrillar, the strands extending outward toward the plasma membrane. In the region of the nuclei and in contact with them are irregular aggregations of material which also stains brightly with ruthenium red, possibly indicating that the nucleus is a source of pectic materials used in wall building. The cell plates round up at the periphery, becoming continuous with the peripheral ruthenium red layer. Each member of the tetrad thus becomes surrounded by a rather uniform, red-staining layer in close contact with the plasma membrane. Just how the plasma membranes adjacent to the cell plates become differentiated from this layer, I have not been able as yet to determine. The red-staining pectic layer is plainly double where contiguous sister cells abut against one another and much thicker than the peripheral layer, though it may appear as a single line except at margins where the cells tend to round up and its doubleness becomes apparent. In their staining reaction these peripheral layers of the tetrad resemble middle lamellae in all respects.

As the pollen tetrads become fully organized the middle lamella of the archesporial cell wall undergoes a very notable metamorphosis. This red-staining layer, which has marked the boundaries of the pollen mother-cells throughout the preceding stages, undergoes a change in its physical state, apparently of the nature of an hydrolysis, becoming more gelatinous in character. It becomes perforated and alveolar, then reticulated, and finally fibrillar, the stages following one another in rather rapid succession. It is apparently viscous and elastic throughout all these stages, but later hardens up and becomes tough and perhaps horny with the ripening of the pollen tetrad. Some of the transition stages in this process are shown in figures 18 and 19 and in the photomicrographs (figs. 30, 31). The middle lamella in the beginning behaves as if it were a soft, gelatinous sheet which is stretched and torn ultimately into irregular threads and strands. Holes of various sizes first appear, these perforations often being so large and numerous that the effect of a network is produced. Torn ribbons or segments of a thin sheet with irregularly torn edges are also formed. Ribbon-like structures, often twisted and frequently of uneven width, are of common occur-

rence. Thread-like strands are widely distributed throughout the anther cavity, running everywhere and joining the other structures. They may be either long or short, wide or narrow, simple or anastomosing. All intermediate degrees of shape and form between threads, ribbons, network, sheets and intact middle lamellae can be found, one arising from another and all more or less connected to form a loose mass of colloidal open-work which is continuous throughout the anther cavity. Frequently the middle lamella appears to be breaking up directly into a fibrillar reticulum through a sort of shredding process. In all cases a reticulum appears to be formed ultimately from the sheets, ribbons and other transitional structures after they become perforated and shredded into a fine network. The material of which these structures are composed continues to stain with ruthenium red as before (fig. 18).

Eventually, as noted, this red-staining, gelatinous material all becomes fibrillar and thread-like through the enlargement of the open spaces in the reticulated structures and the lengthening of the elements into long strands. The fibrils thus formed are of various lengths and sparsely branched, but make up a reticulum consisting of large open spaces and branchings that are far apart. The fibrils composing this reticulum are attached to the special mother-cell walls and are continuous with the middle lamellae of the tapetal cells. There can be no doubt as to their relation with and origin from the middle lamella. Up to this stage these fibrils differ from the mature viscin strands in that they still appear to be more gelatinous and stain more readily.

Immediately preceding and during the disintegration of the middle lamella and the development of young viscin strands, a considerable enlargement of the anther cavity takes place, a marked increase in growth occurring at this time. The cavity doubles its size in all dimensions between diakinesis and the development of the young viscin strands. This enlargement is, of course, the expression of the mass growth of the pollen tetrads and the increase in the tapetal liquid, and brings as its sequence the stretching and alveolation of the middlle lamellae. At the time when the viscin strands are being formed and the middle lamella is breaking up into a reticulum, the latter is still, as noted above, continuous with the red-staining middle lamella material of the tapetal cell walls. As the anther cavity enlarges, the three-dimensional network of middle lamella material, still in a more or less soft and plastic condition, remains connected with the walls of the tapetal cells and the enlargement of the whole system naturally initiates the tearing, shredding, and perforation processes described above. It would seem, therefore, that the enlargement of the anther and

the hydrolysis of the middle lamella are the important factors in bringing about its transformation into the young viscin strands.

When the middle lamella breaks up into fibrils, the tetrads are still enveloped by the orange-staining special mother-cell walls. In fixed material these orange zones are now closely adherent to the peripheral walls of the tetrads (figs. 17, 18, 19) instead of being in contact with the middle lamella and leaving an open zone about the cells as previously (fig. 16). It seems probable that in living material the special mother-cell wall is always in contact with the protoplast and that the separation between orange zone and protoplast shown in the figures is due to shrinkage of the protoplast in fixation. It may be assumed, therefore, that prior to the disintegration of the middle lamella the special mother-cell wall is in contact with both protoplast and middle lamella, and that when the latter becomes dissociated into fibrils the special mother-cell wall remains in its original position around the tetrad. There is no intrusion of the special wall between the daughter cells of the tetrads as figured by Farr (1916).

Soon after the transformation of the middle lamella into fibrils, the orange-staining special mother-cell walls disappear. I have not been able to trace the stages in their disappearance nor the initial stages in the differentiation of the tetrad walls. I have observed no instance in the material studied in which the thickening of the tetrad walls had commenced before the disappearance of the special mother-cell wall. A few anthers have been found in which the special walls have disappeared while no thickening, layers have yet been formed. Although much material has been examined, I have found no definite intermediate stages between those shown in figures 20 and 21.

The secondary thickening layers ultimately formed are found on both the primary peripheral walls and the partition walls of the young pollen tetrad. Around the surface of the tetrad, occupying the position previously held by the special mother-cell wall, is a layer much thinner than the former special wall (compare figs. 20 and 21). This becomes the outer thickening layer of the exine in the cell wall of the mature pollen tetrad. Inside the primary wall is another layer, usually somewhat thicker than that outside, but staining similarly. This becomes the inner thickening layer. It lies in contact with the primary layers of both the peripheral and partition walls alike. The intine has not yet appeared. The primary partition walls between any two contiguous members of the tetrad, although double, remain closely appressed and appear as one solid line without any intrusion of the outer thickening layer between them.

When the walls of the tetrad become thickened, staining becomes more difficult, especially in the case of the walls and fibrils. The thickened walls

stain slightly with orange G at first (fig. 21), but soon stain little or not at all with the common reagents such as haematoxylin, and react as if cutinized. The thread-like strands,which have been formed as described above from the old, ruthenium red staining middle lamella, now stain with great difficulty and react as do the viscin strands of mature pollen. At this time they also appear to have become more solidified, and in their form, size and structure now clearly resemble mature viscin strands.

It has been mentioned that in the earlier stages of their development the viscin strands generally are in contact with the surfaces of the special mother-cell walls. When the outer thickening layer of the exine is formed, the relation of the viscin strands to the latter remains practically the same as the relation between the strands and the special wall. The origin of the viscin strands from the three-dimensional system of middle lamellae implies that the pollen tetrads will lie, as it were, vested or enmeshed in the viscin strand system. The strands come in contact with the tetrads for longer or shorter distances. In the early stages of this contact, when the young viscin strands are somewhat soft and gelatinous, the tetrad walls also may be assumed to be in a somewhat plastic condition. This is indicated by the fact that both strands and walls stain more readily at first than they do subsequently. It seems apparent that in the later stages, when the parts solidify, the viscin strands form permanent attachments to the outer wall of the pollen tetrads, the two becoming welded together, as it were, at all points where they touched and adhered during their previous gelatinous state. An immature pollen tetrad with its viscin strands firmly attached to the surface of the outer thickening layer is shown in figure 22. Other strands, which have not become attached to the tetrad, are also shown. Cross-sections of certain strands which have been cut in sectioning are seen around the periphery of the tetrad as if glued to the surface of the exine.

The intine does not develop until the tetrad nears maturity. Then it appears as a thin layer immediately inside the inner thickening layer of the exine and in contact with the plasma membrane. It is apparently of a pectic material, because it stains brilliantly with ruthenium red. In the mature pollen tetrad it appears as shown in figure 24.

When a ripening pollen tetrad is stained in ruthenium red without sectioning, the first traces of the longitudinal furrows on its surface may be seen as narrow, red lines, indicated diagrammatically in text figure 27 (page 289). Evidently the red staining material is the underlying primary layer of the exine which is exposed when the longitudinal furrows first develop as narrow slits or openings in the outer thickening layer. Nothing else stains brightly with ruthenium red in unsectioned material.

A general increase in the size of the tetrad takes place during the ripening period. Although the pollen is not shed until spring or early summer, the pollen tetrads are practically mature in the autumn, having developed viscin strands, furrows, intine and granular surface. A rapid enlargement of the anther and a considerable enlargement of the tetrad takes place about one week before the pollen is shed. The thickening layers of the exine of mature pollen tetrads are proportionally somewhat thinner than in the half-ripened tetrad (compare figs. 22 and 24).

## MEIOSIS IN RHODODENDRON CATAWBIENSE

I have found no description of meiosis in the genus *Rhododendron* in the literature, nor have the chromosome numbers been reported. I have had abundant material and shall include a brief summary of the stages observed, preliminary to a fuller treatment to be given later. The maturation divisions in the anthers of *Rhododendron* are of the usual type and are very regular in their behavior.

The archesporium consists of several layers of closely packed cells occupying the center of the anther cavity and surrounded by one layer of tapetal cells (fig. 1). The pollen mother cells soon enlarge somewhat and become more rounded in outline, while their nuclei undergo a corresponding increase in size (fig. 2).

With further enlargement of the nucleus, its chromatin assumes a thread-like form, the spireme (fig. 3). The double nature of the threads at this stage is not, however, clearly evident in the material studied. The chromatin threads now thicken and draw together at one side of the nucleus, where they assume the form of a tightly contracted synaptic knot (fig. 4). Later this knot becomes loosened and the strands emerge as an elongated thread distributed rather evenly throughout the nucleus, forming a twisted and interlaced spireme with numerous open loops (fig. 5).

From the open loop condition the chromosomes shorten and thicken still further (figs. 6, 7) and pass into diakinesis. At this stage the pairs lie scattered about the nucleus and are so contracted that their length does not exceed twice their width (fig. 8). They are remarkably uniform in size and shape. They stain readily and may be counted with facility. There are twelve pairs, making the diploid number 24. The various pairs tend to arrange themselves in more or less of a serial order. The bivalent pairs, the members of which lie opposite one another, sometimes show a longitudinal, secondary splitting, so that a pair may appear as a 'chromosome tetrad.' This secondary split, which functions in the homoeotypic division, is frequently evident as early as diakinesis and its presence at this phase operates to make more difficult an accurate counting of the chromosomes,

since it produces the appearance of an increased chromosome number.

The nuclear membrane now disappears and the spindle is formed (fig. 9). The chromosomes become lined up in the equatorial region and the two members of each bivalent pair are drawn toward opposite poles (figs. 10, 11). No cell plate is laid down following this division. The chromosmes are drawn into clusters at each pole (fig. 12) and a nuclear membrane is reconstructed around each group. The homoeotypic division follows very closely upon the completion of the heterotypic telophases.

In interkinesis the chromatin of each nucleus becomes somewhat thread-like but soon contracts and forms twelve chromosomes which arrange themselves on the equatorial plate of the second spindle. A structureless mass of densely staining material is noticeable in the central region of the cell at this stage (fig. 13). The old heterotypic spindle, whose fibers persist through interkinesis, disappears simultaneously with the formation of new spindle fibers. The spindles, upon which the equatorial plates occur, frequently appear nearly parallel at first, but usually become turned until their axes are at right angles to one another (fig. 14).

The twelve chromosomes of each daughter nucleus, which were lined up on the homoeotypic equatorial plate (fig. 13), now divide and the daughter chromosomes draw apart toward the opposite poles (figs. 14, 15). Beside the two spindles of karyokinesis, four other cytokinetic spindles are next formed connecting the poles of opposite karyokinetic spindles, as shown, in part, in figure 14. There are thus six spindles in the pollen mother-cell in the homoeotypic telophases, four serving solely for the laying down of cell plates. As the divided chromosomes reach the poles and begin to reconstruct themselves into daughter nuclei, a definite cell plate is laid down in the equatorial region of each of the six spindles in the pollen mother-cell. The cell plate first appears as a series of small dots or enlargements (fig.16) which soon coalesce into a solid line. This is followed, or accompanied, by the formation of a thin membrane of similarly staining material around the entire periphery of the tetrad.

At the conclusion of the second, or homoeotypic division, therefore, each of the original pollen mother-cells has become a tetrad consisting of four daughter cells, separated from one another by definite partition walls and all united within one peripheral wall which completely encompasses them, constituting a figure which approximates the form of a tetrahedron with bulging faces (fig. 20). The tetrad walls have no visible thickening layers at this stage and they are separated from the archesporial cell walls by a special, gelatinous sheath, the special mother-cell wall. No further division of the nuclei takes place until after the germination of the mature pollen tetrad.

In addition to the chromosome counts made from imbedded and sectioned material of *Rhododendron catawbiense*, preliminary counts, using Longley's acetocarmine technique, were made from fresh material of *R. maximum*, *R. carolinianum*, *R. calendulaceum* and *R. arborescens*. These all appear to have twelve chromosomes in the haploid condition. In the hybrids examined, the same number was found.

During meiosis the tapetal cells are very active. At the heterotypic division they become binucleated. They stain densely during the period of their activity and finally collapse at or about the time of the homoeotypic telophases, but do not completely disintegrate until later.

## REVIEW OF THE LITERATURE

The viscin strands of *Rhododendron* pollen have, in the past, been little observed, doubtless owing to their lack of staining capacity. The strands are conspicuous in dry material, but they are somewhat difficult to see under ordinary powers when mounted in liquids.

It was probably the Danish botanist, Rafn (1796), who first reported viscin strands on the pollen grains of *Impatiens balsamina*. Rafn speaks of the pollen grains as bound to one another by fine threads or strands, so that they look like beads hung loosely on a string. Link (1807, p. 215) noted that such fine strands are more distinct in the pollen of *Oenothera* than in that of *Impatiens*.

Mirbel (1815) described and figured the pollen of *Rhododendron viscosum*, showing the compound grain and the viscin strands. Mirbel evidently did not recognize the tetrahedral arrangement of the microspores and showed only three-celled groups in his illustration. Yet he must have recognized the four-celled character of some of the tetrads, since he described the pollen of this species in the following words: 'Grains de pollen trilobés et quadrilobés.' Mirbel noted that the pollen groups are joined together by delicate strands in several members of the Ericaceae, as well as in the Onagraceae. The pollen grains, he said, 'sont attachés les uns aux autres par des fils d'une extrême ténuité dans le *Rhododendrum*, *l'Azalea*, *l'Epilobium*, le *Gaura*, la Balsamine, etc.'

Purkinje (1830) gave figures of pollen tetrads in three members of the Ericaceae, including *Rhododendron luteum*. In every case, all four microspores were shown, but there is no indication of viscin strands in the illustrations. He noted that compound pollen grains are especially common in the Ericaceae.

Fritzsche (1832) figured the pollen of *Rhododendron indicum*, plainly showing the pollen tetrads with their longitudinal furrows, but failing to depict or describe the viscin strands. Von Mohl (1835, p. 148, 232, 317) in

his classification of pollen grains, distinguished the germinal furrows of ericaceous pollen and figured a longitudinal furrow with two germinal apertures near its center, these being separated only by a crosswall. He did not perceive the transverse furrows, however, nor did he show the viscin strands. Klotzsch (1851) mentioned the delicate threads, and Gray (1878, p. 14) used the compound pollen grain as a family character for the Ericaceae, as also did Drude (1889, p. 35) in Engler and Prantl. Schürhoff (1926) however, has stated that in one species, *Erica stricta*, the microspores of the mature pollen are separate and do not adhere in tetrads.

Nägeli (1842), in his work on pollen, makes no mention of viscin strands nor do these structures appear to have been noted, in ericaceous plants, at least, by Edgeworth (1876) in his later book on pollen. W. G. Smith (1876) figured the pollen of *Rhododendron catawbiense* and mentioned its 'viscid threads.'

Strasburger (1882) in his 'Zellhäute' described exine development in many genera, but did not treat of any ericaceous plants nor mention the presence of fibrils in *Oenothera*, which, while not fully comparable to those of *Rhododendron*, are of interest in this connection.

Wille (1886) studied the thickening of the microspore walls and the development of the outer surface of the pollen grains in representatives of several genera, among them *Erica*. Pollen of this genus bears no viscin strands, but Wille figured the pollen tetrads and described the special mother-cell wall. He also considered the method of thickening of the microspore walls, which he held was by intussusception. Wille finds that if one presses upon a tetrad which is surrounded by a special mother-cell wall, the latter is pushed away from the periphery of the tetrad except at the points of contact with the partition walls (septa), where V-shaped extensions of the special wall, much like those later described by Farr (1916) in quadripartition by furrowing, extend directly into the septa. This work was done on *Erica denticulata* and *Drimys Winteri*, and a schematic diagram was given to show that the partition walls are thickened by the incorporation of substance from the special wall. I have endeavored to duplicate Wille's experiment, using *Rhododendron catawbiense*, but have not been able to confirm his results. In no case, when pressing upon a tetrad, have I observed the special mother-cell wall to remain adherent to the partition walls when loosened from the peripheral walls.

I find, however, that in young *Rhododendron* tetrads individual microspores may sometimes be made to free themselves from their connection with the other members of the quartette when heavy pressure is applied, a split occurring in the partition walls. This indicates that these walls are

double. It seems probable that Wille induced by pressure a split in the partition walls, and that material from the special mother-cell wall flowed into the spaces thus opened.

Strasburger (1889) amplified and extended his earlier observations on the development of pollen cell walls. He discussed ericaceous pollen and figured a germinal furrow on the pollen of *Erica tetralix*. He did not observe, however, the transverse furrows, depicting only the longitudinal furrow in his figure. He did not work with ericaceous forms having viscin strands, and does not mention these structures. Nor did he mention or figure fibrils of this nature among the Onagraceae, or for any of the other pollen-bearing plants described. Strasburger studied the thickening process in the walls of the pollen tetrads of *Erica*, and concluded that it is similar to the production of a thickening layer on an ordinary cell wall. He notes that the walls react as if cutinized as soon as they become thickened. Strasburger (1898), speaking generally, states that the walls of a pollen grain may develop either by the embodiment of substance (intussusception) or by the laying on of substance (apposition), or by a combination of both processes. In an earlier work, Strasburger (1884, p. 507) described the pollen tetrads of *Rhododendron* and the structure of the anther, but did not mention viscin strands. Fischer (1890) also failed to discuss the viscin strands.

Kerner (1891) figured the pollen tetrads of *Rhododendron hirsutum* with their viscin strands. He spoke of a 'sticky, structureless substance' adhering to the pollen tetrads, and said (Oliver's translation):

> This substance does not form droplets with water nor does it dissolve in alcohol and olive-oil. It may be termed *Viscin*, from the similarity which it presents to the bird-lime obtained from the berries of the mistletoe (*Viscum*). Such a viscin is met with on the surface of the pollen grains . . . . throughout the Onagraceae and in Azaleas, Rhododendrons, Orchids and Asclepiads. It is very sticky, and on the slightest touch can be drawn out into delicate threads. The contents of the anthers, as they escape, in the Evening Primrose (*Oenothera*) and Willow-herb (*Epilobium angustifolium*) resemble fringes and tattered ribbons, or a broken net hanging from the adjacent anthers. Under the microscope this substance is seen to consist of pollen grains, joined together by sticky strings of viscin. . . . . In *Rhododendron hirsutum* all the pollen tetrads of an anther cavity are held together by a mass of sticky viscin. The anther dehisces by two terminal pores, and from these the pollen tetrads ooze out to some extent. If the sticky mass be touched with a bristle it adheres, and the whole contents of the anther can be readily withdrawn. . . . . The sticky substance is probably a mucilage formed from the outer wall of the pollen tetrad, or from the broken-down walls of the mother-cells.

The question of whether these structures in all the widely separated families named are strictly comparable, needs further study. I have been unable to determine whether or not the term 'viscin' originated with Ker-

ner, but this appears to be the case, although Smith (1876) spoke of 'viscid threads,' as noted, some fifteen years earlier. The term *viscin* has since been used rather generally in referring to the strands and fibrils found on the pollen tetrads of *Rhododendron*. It should be emphasized, however, that the term *viscin* is now applicable only in its historical sense as a name for these structures and not with reference to their formerly supposed viscid nature.

Beer (1905) reported that

> the mature pollen grains of *Oenothera* are bound together in long strings by bundles of 'fibrils' which lie between and round them. These fibrils are developed from the mucilage which . . . . we saw was derived from the disintegration of the special mother-cell walls. These fibrils have entirely lost all affinity for callose dyes and have become very resistant to solvents. Their properties in many respects resemble those of cuticularised structures. When the special mother-cell wall breaks down it forms at first a structureless mucilage which no longer gives any of the reactions of callose. Later this mucilage becomes drawn out into 'fibrils.'

Beer does not figure the process of fibril development.

In a later paper, Beer (1911) described the special mother-cell wall of *Ipomoea* as a 'massive mucilaginous wall' surrounding the tetrad, having the staining qualities of Mangin's callose and pectose. Each microspore here has, in addition, a special mucilaginous wall of its own and the protoplast deposits a delicate layer on the inner face of this callose-pectose wall, this thin layer becoming the exine. A net-like structure develops on the inner surface of this young exine bearing the rudiments of future spines. Thickening bands in this region enlarge by secretion from the protoplast. Soon the special walls 'break down into a diffuse, flocculent material, which fills the anther cavity. The spines now project above the outer surface and the young pollen grain increases in size rapidly, apparently receiving material from both outside, as evidenced by tapetal activity, and from within the protoplast, as evidenced by changes in alveolation and in the size of the nucleoli. The intine develops late as a thin layer on the inner surface of the wall, probably by apposition of materials from within.

Farr (1916) studied cytokinesis in pollen mother-cells and concluded that the special mother-cell wall was derived, through swelling and thickening, from the secondary strata of the original mother-cell wall. He describes it as homogeneous and as staining with orange, and suggests that it is a transitional form of carbohydrate, such as (quoting Timberlake) a carbohydrate 'in the process of polymerization from a soluble sugar of low molecular weight through the less soluble dextrins, etc., and ultimately into cellulose.' It may be passing through transitional stages, Farr said,

'leading ultimately to its dissolution and disintegration. This thickening of the mother-wall is probably in the nature of a colloidal swelling or hydration .... which process .... ultimately leads to such extreme dispersity that an entire dissolution of the mother-wall ensues.'

Gates (1925), describing the special mother-cell wall in *Lathraea*, considered that this heavy special wall is a secretion from the cytoplasm, independent of the archesporial cell wall, although laid down in contact with it. He stated that the increase in thickness is not due to swelling, as Farr contended, because its various parts are unequal in thickness and that thin orange zones, no denser than the others, are first laid down and gradually become thicker, presumably by deposition. The special mother-cell wall dissolves and disappears, according to Gates, soon after the archesporial cell walls disintegrate. By this time each young pollen grain has formed its own wall from within.

Castetter (1925), working on the pollen mother-cells of *Melilotus*, found, as did Wille, that the special mother-cell wall is first seen only at the angles of the pollen mother cell. As in *Rhododendron*, it appears first during synizesis. It reacts as pure callose and stains with orange G. An inner special callose wall, denser than the outer one, is formed around each microspore in *Melilotus*. These special walls ultimately break down and disappear.

The composition of cell walls, including the walls of pollen grains, was studied by Mangin (1888–93, 1889, 1892, 1893), who pointed out the value of ruthenium red as a differential stain for pectic compounds. He found that this stain would color the mucilage of certain seeds, the gums from cycads and fruit trees, the gelatinous membranes of the pollen grains of *Juniperus*, *Taxus*, *Iris* and *Narcissus*, and certain algae and bacteria. He reported the presence of pectic compounds in the middle lamellae of cell walls and in the intine of pollen grains. Nitrogenous materials, he found, might become weakly colored with ruthenium red, but are stained more strongly by methylene blue. Mangin emphasized the important rôle which pectic compounds play, the large number of forms which they may assume, and the transitional nature of many of the substances found in plant tissues.

The researches of Mangin were extended by those of Biourge (1892), who studied the form and composition of the pollen walls of several genera. Fitting (1900) made important contributions to the knowledge of spore wall formation in *Isoetes* and *Selaginella*. Timberlake (1900) found that the middle lamella appears to be formed after the splitting of the cell plate, by material which is deposited between the split halves. Orange staining material, present near the equatorial region in the dividing root cell of the

onion, was thought by Timberlake to undergo a transformation into cell wall material. The work of Allen (1901) confirmed the conclusions of Mangin regarding the presence of pectic compounds in the middle lamella and showed that the middle lamella consists of the layers first deposited by the plasma membrane, plus a certain amount of material subsequently deposited in contact with these layers and generally rich in pectic compounds.

## DISCUSSION

*1. The origin of viscin strands.* That the viscin strands originate from material of the primary bounding membrane of the archesporial cells appears evident. This material stains, at first, as if it were a pectic compound characteristic of the middle lamella. The strands may be fully formed while the special mother-cell walls are still present, and hence they do not, in *Rhododendron* at least, take their origin from the mucilaginous material of the special mother-cell walls as Beer (1905) has reported for *Oenothera*. Moreover, tests with ruthenium red and orange G, at the time when the strands are being formed, reveal no traces in them of the orange staining material of the special walls, thus indicating that the substance forming the fibrillar reticulum is that of the red-staining middle lamella only. The rapid enlargement of the anther cavity, plus the water relations within the anther at this time and subsequently, are doubtless important agencies in bringing about the disintegration of the mother-cell walls and the metamorphosis of the middle lamella into fibrils and thread-like strands.

The stages in this process are, as noted: first, the formation of perforations and alveolations; second, the tearing and shredding of the middle lamella into irregular strands and ribbons which thus becomes a fibrillar reticulum of three dimensions; and finally, the lengthening of the fibrils to form a continuous system of long, sparsely branched viscin strands. These transformations are not inconsistent with our present knowledge concerning the structure of cell-wall materials and the general properties of colloids. It is a familiar fact that colloids may show vastly different structural characteristics under changing environmental conditions, especially those of moisture, temperature and tension, not to mention phase reversals. One can readily interpret the alveolar and reticulated condition of the disintegrating middle lamella as a transition stage between the original dense, 'set' condition (gel) of the primary wall and a later solid, gel condition attained when the viscin strands are fully mature. It seems probable that the middle lamella imbibes water, with the result that it undergoes a change in structure—a change from a solid, gel condi-

tion to a more dispersed, less solid state by which it passes from a gel toward a sol, without, however, attaining more than a partial transition to the fluid state, the result being a somewhat viscous colloidal structure. Stretching from the growth of the anther, results in the alveolated and then netted condition as a three-dimensional reticulum. In *Rhododendron* the transition toward a liquid state stops at this point, while in other genera, as described by numerous writers, the disintegrating mother-cell walls appear to break down completely into a fluid state and disappear.

Ultimately the viscin strands, formed out of the broken down middle lamella, solidify, and this process is accompanied by a general change in staining reactions throughout the entire anther cavity, indicating that this gelation is in the nature of a physio-chemical change associated with the process of ripening. It is not improbable that the water relations of the anther wall play a large rôle in these stages. The mechanical influence of enlargement and stretching is, however, the prime factor in changing the membranous middle lamella into the three-dimensional reticulum of the viscin strands.

That the mature viscin strands do not possess the sticky qualities attributed to them by Kerner (1891) is entirely evident. The attachment of the strands to the pollen tetrads at points where the two are in contact during the ripening period, and their permanent adhesion through a sort of welding process are in keeping with the conception of a general solidification of parts at that stage. Thus, we may say that in the complete transformation from the middle lamella to the viscin strand there has been, first, a transition from a gel to a viscous condition, followed by another change back again to the condition of a gel.

*2. The function of viscin strands.* The viscin strands of *Rhododendron catawbiense* obviously function as adaptive structures for insect pollination. According to Müller (1883) and Knuth (1908) the flowers are regularly visited by several species of bees which touch the protruding wefts of pollen with their bodies, withdraw it from the anthers and carry it to other flowers where cross-pollination takes place. It has been shown by Comber (1925) and Bowers (1927a, b) that many rhododendrons, including *R. catawbiense*, are self-incompatible, so that the advantage of cross-pollination is obvious. The entire contents of an anther lobe may be removed at one time.

It has been noted by Matthews and Knox (1926) that the staminal apparatus of the Ericaceae is quite specialized and is in advance of other characters accepted as criteria for placing the family at the beginning of the sympetalous dicotyledons. In most genera of the Ericaceae the flowers are pendulous, the corollas are more or less closed, and there are no viscin

strands, yet the stamens are adapted for insect pollination either through special appendages, as spurs and awns, or by adjustments of their length. Except in the apparently primitive forms, such as *Elliottia*, *Cladothamnus*, and *Loiseleuria*, no normal longitudinal dehiscence of the anthers is found. In the subfamily Rhododendroideae there is no hypodermal fibrous thickened layer, or endothecium, to function as a hygroscopic mechanism in bringing about dehiscence of the anther. From the primitive type, according to Matthews and Knox, the *Rhododendron* group seems to have followed a specialized line of staminal development, differing from the line followed by other members of the family. The flowers of the rhododendrons are large, open, and relatively erect, in contrast with the pendulous and semi-closed habit of the others. With apical, porose dehiscence and the tetrads in a loose, powdery condition, the pollen could not be advantageously shed nor effectively applied to insects. The viscin strands are adapted to just these conditions.

*3. Development of the pollen tetrad walls.* The progressive stages in the development of the primary walls of the pollen tetrad are well shown in my material. The primary peripheral wall of the tetrads, which appears as a red-staining line soon after cell plate formation, appears to be of the same material as the partition walls with which it is continuous. The partition walls are formed from a cell plate, while the peripheral walls arise without visible association with cel plate or spindles, although part of their substance may come from fibers of the cytoplasm, since these are present in excess of requirements for cell plate formation. The peripheral walls seem to arise immediately outside the plasma membrane and are perhaps formed out of pectic substances derived from the region of the nucleus. Fibrillar strands of cytoplasm (kinoplasmic fibers), radiating toward the periphery at this stage, may be concerned in the conduction of this material toward the plasma membrane. The staining reactions of the primary walls of the tetrad are thus similar to those of the archesporial cell walls.

The thickening of the tetrad walls in *Erica tetralix* was studied by Strasburger (1889), who observed the similarity of the thickening layers of pollen tetrads to the corresponding layers of other cell walls, and noted that the tetrad walls react as if cutinized soon after becoming thickened. Fitting (1900) and Strasburger (1907) demonstrated that in certain cases development of the exine may proceed without contact with the protoplast, being apparently to some extent derived from materials outside the cell. Strasburger's early view was that all cell wall materials were products of the protoplast. The work of Beer (1911) indicated that the formation of pollen grain walls in *Ipomoea* is initiated and directed by protoplasmic activity within the grain, but that subsequent growth in substance of the

outer wall surfaces and their sculpturings may be carried on by the addition of materials from outside. In *Rhododendron* the development of secondary thickening layers on the exine proceeds with great rapidity, and I have not, as yet, been able to clearly trace its stages.

The work here reported was done n the laboratories of the New York Botanical Garden. It is a pleasure for me to express my appreciation to Dr. A. B. Stout and Professor R. A. Harper for their valuable guidance and kindly criticism during the course of these studies and in the preparation of this paper.

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## Explanation of plates 11–15

All drawings were made with the aid of a Zeiss binocular research microscope, model FCE-6, apochromatic objectives: 3mm. n.a. 1.3 and 2mm. n.a. 1.4; oculars: 7, 10, 15, and 20, giving magnifications up to 1800 diameters. Except where otherwise noted, the drawings in plates 11, 12, and 14 are here reproduced at a magnification of approximately 2,000 diameters; those in plate 13 at a magnification of 2300 diameters. Measurements were made with a Stufen ocular micrometer 2.

### Plate 11

Fig. 1. Pollen mother-cell, archesporial stage.

Fig. 2. Pollen mother-cell rounding up and enlarging.

Fig. 3. Nucleus at the spireme stage, before synizesis.

Fig. 4. Synizesis.

Fig. 5. The open spireme stage, following synizesis. First appearance of the special mother-cell wall as orange-staining, gelatinous material in the angles of the cell. The protoplast has contracted away from the cell wall.

Figs. 6 and 7. Stages between open spireme and diakinesis. The special mother-cell wall is now present as a massive gelatinous sheath enveloping the protoplast.

Fig. 8. Diakinesis, showing 12 pairs of bivalent chromosomes, some in form of 'chromosome tetrads.'

Fig. 9. Heterotypic metaphase.

Figs. 10 and 11. Heterotypic anaphases.

### Plate 12

Fig. 12. Heterotypic telophase.

Fig. 13. Homoeotypic metaphase.

Figs. 14 and 15. Homoeotypic anaphases. Two karyokinetic spindles and four cytokinetic spindles are now present.

Fig. 16. Homoeotypic telophase. Cell plates now forming partition walls between daughter nuclei.

## PLATE 13

Fig. 16a. The archesporial cell walls and special mother-cell walls as they appear when stained with ruthenium red and orange G. The cytoplasm, nuclei, spindle fibers and other contents have been omitted from this drawing as they are not clearly differentiated by this stain.

Fig. 17. Tetrad, showing formation of partition walls. The septa stain readily with ruthenium red and appear as if double. The peripheral wall is beginning to appear as a single, thin, red membrane. The cytoplasm is fibrillar and extends outward from nucleus toward periphery. Red-staining material appears about the peripheries of the nuclei.

Fig. 18. The disintegration of the archesporial cell walls to form a reticulated network and finally viscin strands. Intermediate stages between intact middle lamellae and thread-like fibrils are shown. A segment of intact middle lamella is conspicuous in the lower left-hand corner of the drawing. Stained with ruthenium red and orange G.

Fig. 19 (plate 12). Disintegration of archesporial cell walls to form viscin strands, showing relations of walls, tetrads and fibrils. Stained with Delafield's haematoxylin and orange G. ×1000.

## PLATE 14

Fig. 20. Young pollen tetrad, showing unthickened primary walls surrounded by special mother-cell wall.

Fig. 21. Tetrad after special mother-cell wall has disappeared and secondary thickening layers have arisen outside and inside the primary walls. Segments of viscin fibrils are adherent to the outer surface of the tetrad.

Fig. 22. Tetrad at a later stage, its walls much thickened. Viscin strands are shown adherent to the surface of the tetrad and near it.

Fig. 23. A mature pollen tetrad in cross-section. ×330.

Fig. 24. Portion of a mature pollen-tetrad in cross-section, showing the intine, the inner thickening layer, the primary wall and the outer thickening layer. The intine is prominently thickened and protrudes outward at the germinal apertures.

## PLATE 15

Figs. 28 and 29. Photomicrographs showing mature pollen tetrads of *Rhododendron catawbiense* with their viscin strands, ×170.

Figs 30 and 31. Photomicrographs showing disintegration of middle lamellae and formation of alveolated and reticulated network which subsequently becomes fibrillar and solidifies into viscin strands. Fig. 30, ×300; fig. 31, ×150.

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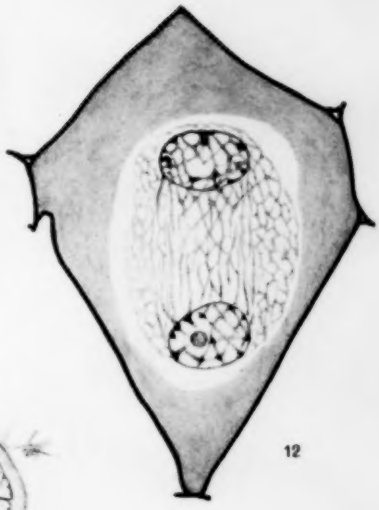

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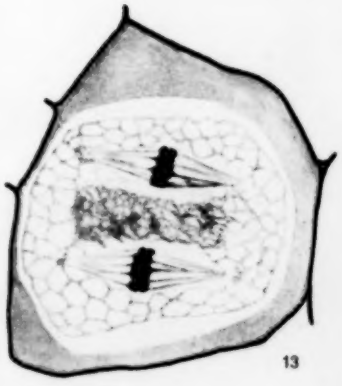

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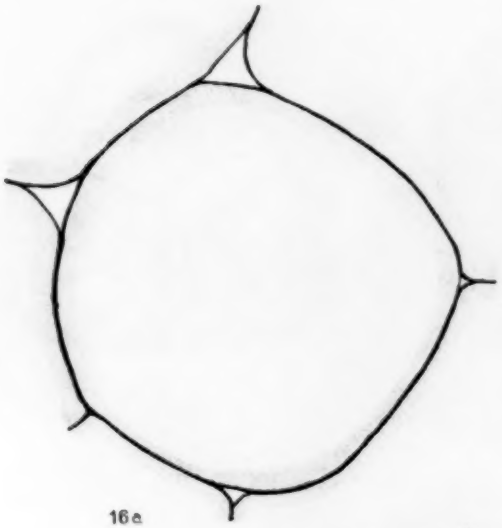

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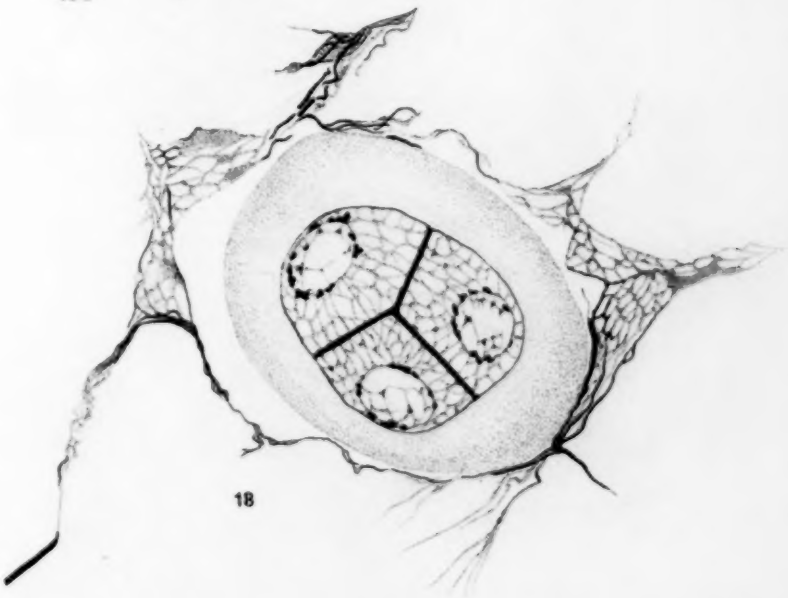

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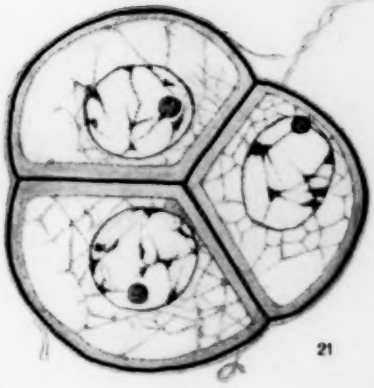

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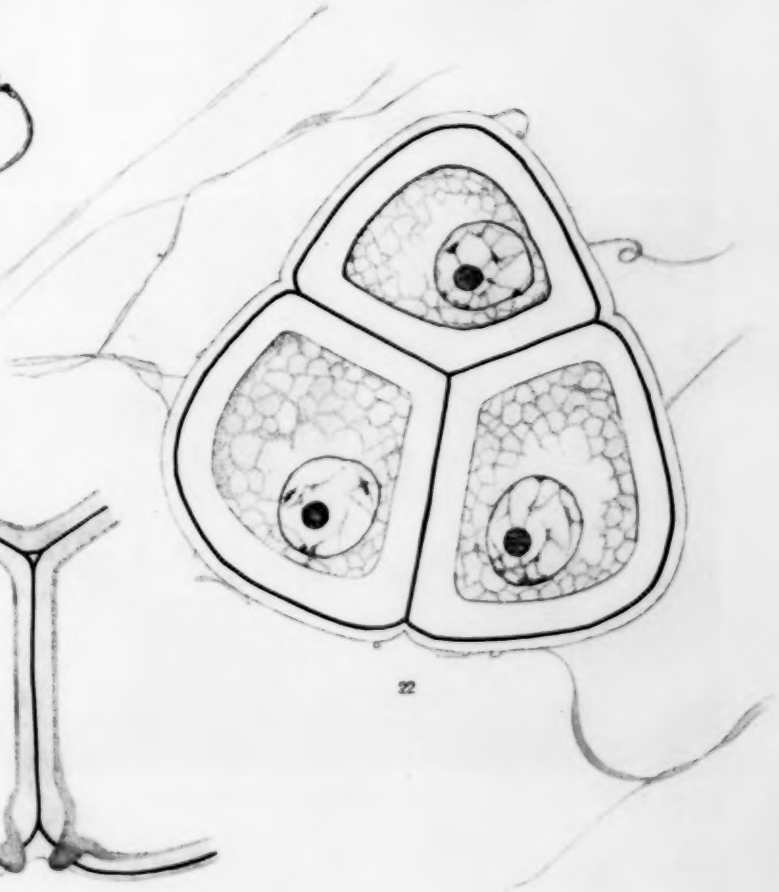

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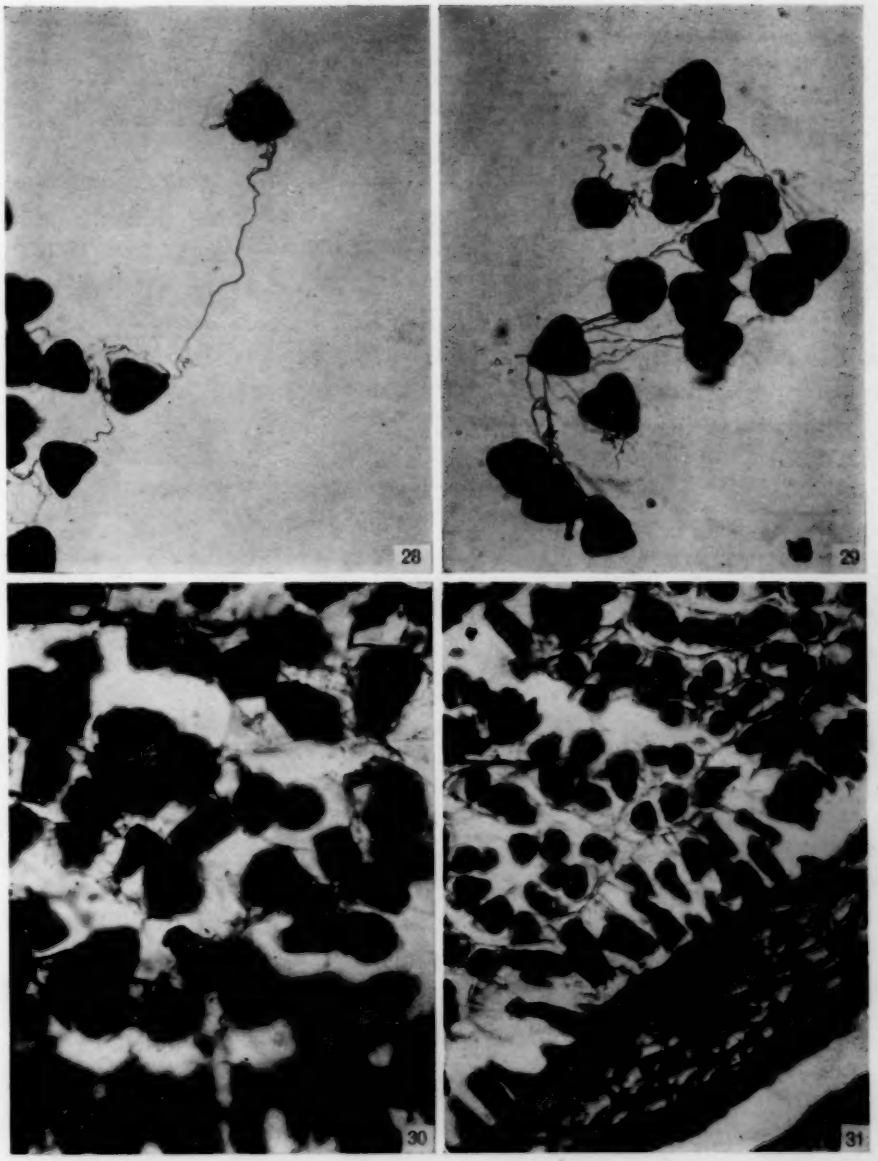


BOWERS: POLLEN IN RHODODENDRON

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# Studies on the morphology of the Onagraceae
## IV. Stenosiphon linifolium

DONALD A. JOHANSEN

(WITH PLATE 16 AND TWENTY-FIVE TEXT FIGURES)

In the first paper of the present series I dealt with a genus which is apparently at the proximal end of an evolutionary group (Johansen 1929 a, b). Before discussing the genus at the presumed distal extremity (*Burragea*), it seems expedient to devote some attention to a somewhat intermediate genus which shows a close affinity to both of the widely separated genera and forms a connecting link between them. Of the two genera which might be discussed, namely, *Heterogaura* or *Stenosiphon*, the latter will be considered as it is the only one of which I have been able to obtain material.

*Stenosiphon* has generally been considered a monotypic genus, the species, *S. linifolium* (Nutt.) Britton, having a rather restricted geographical distribution, with centralization in Oklahoma. However, in the Dudley Herbarium there is a sheet bearing the label '*Stenosiphon bracteatus* n. sp. Jones. Leon Springs, Bexar Co., Texas. June 7, 1911. Coll. by Mr. and Mrs. J. Clemens.' Specimens from the same collection are said to be in other herbaria. There is no record of the publication of this name; a careful comparison of the specimen with a large number of collections of *S. linifolium* from many localities leaves me in doubt as to the justification for the erection of another species.

### MATERIAL AND METHODS

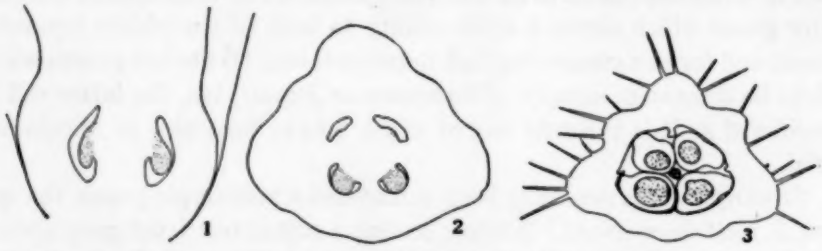
The material studied was obtained from six plants sent me in the spring of 1928 by Mrs. Neva C. Belew of Harmon, Oklahoma. The plants were secured from the prairie in the neighborhood of Harmon.

The younger stages in the development of the ovules were followed out in material intended for the study of microsporogenesis, as the ovaries at this time are too small to be handled conveniently. As soon as they had attained a sufficient size, the ovaries were treated individually. All fixations were in Petrunkewitsch's fluid, this solution penetrating the hard ovarian walls with ease. The fixation was checked in a modified formalin-acetic acid-alcohol and in Flemming's stronger fluid, but these were both inferior to the one first mentioned.

### THE OVARY

The ovary is somewhat flattened on one side; in other words, in transverse section it appears triangular rather than quadrangular or circular in

outline. This flattish side is towards the central stem to which the ovary is attached. The ovary is sessile and on the outer side at the base is compressed to a considerable extent by the subtending bract. The four locules, each containing a single ovule, are so disposed that two are towards the stem, and, on account of the basal compression, the inner two ovules are considerably below the horizontal level of the outer two (fig. 1). The latter, in consequence of being nearer to the apex of the ovary, might be supposed to have a decided advantage at the time of fertilization, but, as will presently be shown, it is one or the other of the two inner and lower ovules




Figs. 1–3. The ovary. 1. Longitudinal section of very young stage. ×60. 2. Transverse section of a slightly later stage, showing triangular outline of ovary. ×60. 3. Transverse section at time of fertilization, showing practical disappearance of locular walls and placenta. ×45. Nucellar cells are stippled.

which contains an embryo. The axile placenta is prominent during the earlier stages of development, but by the time the megagametophyte is ready for fertilization it has almost completely disappeared, owing principally to its inability to keep pace in growth with the rapid lengthening of the ovary (fig. 2). The four ovules remain attached to the quasi-permanent uppermost portion of the placenta, each by means of a rather long funiculus which is right-angled immediately before joining the placenta. The ovary consequently becomes 'one-celled' when mature. Britton and Brown (1897) describe the fruit as being 8-ribbed, but only five of the ribs are prominent enough to be readily distinguishable (fig. 3).

## THE OVULE

The ovule originates and develops in essentially the same manner as has already been described in preceding papers of the present series. The only divergence noted is that the primary archesporial cell and the inner integument, which arise simultaneously, originate at a comparatively late period. That is, the ovule has made a more extensive growth than is the usual case before the megasporocyte can be recognized.

One of the most striking morphological characteristics of this species consists in the development of a dense, tangled tuft of hair-like cells on

the upper part (the short arm) of the angled funiculus, which becomes slightly swollen, with hypertrophy of the individual epidermal cells. These cells resemble fungal hyphae more than anything else; while the majority are rather short and very crooked, non-septate, uninucleate, and contain a thin, principally peripheral cytoplasm, they may occasionally send out short lateral protuberances or even branch dichotomously. They extend far up into the apex of the ovary, packing it tightly until after fertilization, and there is definite proof that the microgametophyte does not travel down the placenta as ordinarily happens, but breaks through at the apex of the ovary and passes through these hair-like processes to the micropyle.

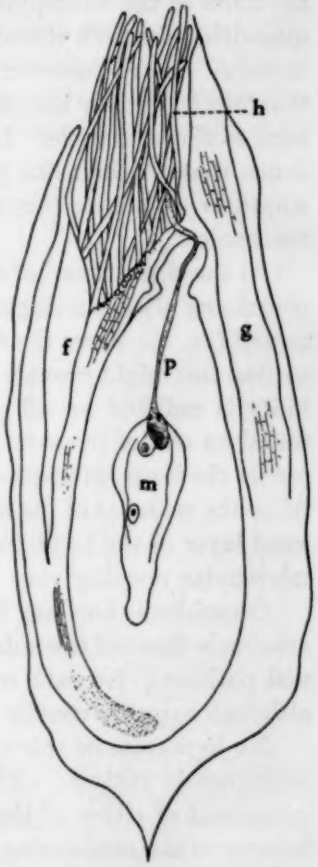



Fig. 4. Outline of ovule at time of fertilization, median longitudinal section. *f*, funiculus; *g*, back of raphe of neighboring ovule; *h*, hairs of funiculus; *m*, megagametophyte; *p*, microgametophyte in tapetal part of nucellus. ×300.

During the growth of the ovary these hairs lengthen correspondingly and may very rarely become rather straight. An exceptional case is portrayed in figure 4. Just before the embryo is ready to begin cotyledon development, the hairs are comparable in length to those comprising the coma in species of *Zauschneria* or *Epilobium*, but in the latter genera it will be recalled that the hairs are at the chalazal end of the ovule in intimate connection with the hypostase and are very regular in organization. There is no similarity or analogy between the two types. Immediately after fertilization the hairs in *Stenosiphon* are narrow in places and considerably swollen elsewhere; branching is very irregular, the nuclei may rarely multiply, and the cytoplasm becomes reduced to small remnants surrounding each nucleus or disposed elsewhere. In those ovules in which the latest stages of embryo development were observed, the hairs seemed to be undergoing partial dissolution, perhaps they may eventually disappear after the seed ripens.

Although here reported for the first time for the Onagraceae, these curious funicular hairs are known in other families, notably among the Um-

belliferae (e.g., Cammerloher, 1910; Håkansson 1923), in *Acer* (Taylor, 1920), and in *Trichosporum* (=*Aeschinanthus*) (Hildebrand, 1872). These writers are all agreed that the microgametophyte grows down through the hairs to the micropyle, and in addition Håkansson believes the large quantities of starch stored in the hairs surmounting the funiculus of *Hydrocotyle vulgaris* nourish the microgametophyte, and Taylor supposed that 'the hairs may secrete a fluid which aids in the passage of the pollen tube to the micropyle.' In *Stenosiphon* I have not found convincing evidence that the hair-like processes secrete a fluid, nor is starch present; whatever assistance they afford the microgamtophyte is probably purely mechanical.

At the chalazal end of a number of ovules a curious columnar structure, containing always a single large deposit of calcium crystals, has been observed (fig. 5). From the fact that it has been found only on non-fertilized ovules, this might provide a means of identifying the latter, but this possibility is nullified for all practical purposes because the structure is not found on ovules in every ovary. At the micropylar end of each of the ovules the inner integument is prolonged into a beak-like process (fig. 6). After the entrance of the microgametophyte, some of the cells of the innermost layer of the fertilized ovule become hypertrophied, thus closing the micropylar opening very effectively.

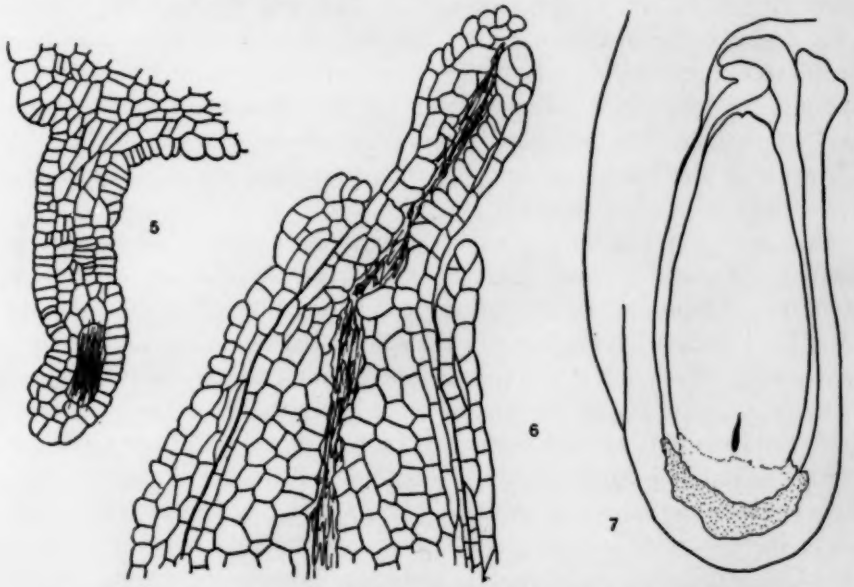
Occasionally one may find one of the four ovules so oriented that its micropyle is directed towards the base of the ovary, in the reverse of the normal position. No such ovule has ever been seen to contain an embryo, although hairs are usually developed upon its funiculus.

No hypostase or epistase is present; the obvious fact that the ovule is permanently enclosed within the ovary removes the necessity for the development of either of these structures for the preservation of the water balance of the seed during the resting period.

The hairs from a particular ovule, almost invariably one of the two innermost, ocupy more of the space in the beaked apex of the ovary than do those of any of the other three ovules. Obviously, the microgametophyte is likely to enter the hairs of this particular ovule, which would then be the only one fertilized. If this is not the determining factor, it is entirely by chance which ovule receives the apparently single microgametophyte to enter the ovary. It is impossible during pre-fertilization stages even to guess at which ovule will become the seed. There is no wholly satisfactory criterion, such as slightly larger size, a perfectly organized megagametophyte, or more abundant funicular hairs, etc. Nor has it been possible to discover the reason why one microgametophyte, and one only, ever enters the ovary; so far as this particular aspect is concerned, the ovary of *Steno-*

*siphon*, in spite of its having four ovules, is analogous to a single ovule in a multiovulate genus such as *Hartmannia*, or to the uniovulate ovary of *Circaea*.

All four ovules, except where on or two possess aborted megasporocytes (fig 7) or quartets, develop at the same rate until shortly after fertilization, whereupon the unfertilized ovules immediately collapse as if they had become desiccated. The process commences with the collapse of the entire nucellus, which is reminiscent of, if not homologous to, the same




Figs. 5–7. 5. Columnar structure at chalazal end of ovule. ×225. 6. Development of inner integument into beak-like process, with hypertrophy of inner layer of cells just beginning. Course of the microgametophyte is evident. ×225. 7. Diagrammatic longitudinal section of ovule with aborted megasporocyte. ×120.

phenomenon in species of other genera, such as *Taraxia* and *Clarkia*. The embryo-containing ovule grows so rapidly through an enormous increase in the number of nucellar cells that it soon occupies all the available space within the indehiscent ovary.

## MEGAGAMETOGENESIS

Nothing particularly noteworthy was observed in the development of the megasporocyte, outside of its unusual lateness in origin. No reason can be assigned for this peculiarity.

Whether or not it might be said to be due to the cumulative effects over a long period of years of the failure of fertilization in all save one of

the ovules, the fact remains that in a great many ovaries there are one or sometimes two ovules in which the megasporocyte never undergoes meiosis. The cell merely lengthens slightly with the growth of the ovule and finally disintegrates (fig. 6). The two outermost ovules are the more likely to show aborted megasporocytes or quarters.

As in other onagrads, a linear row of four megaspores is produced as a result of meiosis. During the progress of the second meiotic mitosis, however, a wall is frequently not organized in the chalazal secondary megasporocyte (pl. 16, fig. 1). This apparently results in the majority of cases in the degeneration of all three cells. The four megaspore cells comprising the quartet are early isolated completely from the neighboring nucellar and tapetal cells, which places them within the boundaries of the embryo sac (pl. 16, figs. 2, 3). That megaspore nearest the micropylar end of the ovule is invariably the functional one; the non-functional megaspores usually persist until after fertilization.

One-, two- and four-nucleate megagametophytes follow the typical developmental stages in every particular, but the organization of three of the four nuclei into synergids and egg cell is irregular. The difficulty patently lies in faulty development of the spindle between the two sister synergid nuclei, occasioned in the first instance by metabolic disturbances in the cytoplasm (pl. 16, fig. 5). One is more likely to find gametophytes in which the synergids are not organized into definite cells, their nuclei remaining naked and the egg nucleus is bounded, in the lower part at least, by a simple protoplasmic membrane (pl. 16, fig. 7), or in which organization of the synergids is incomplete and the egg nucleus remains as destitute of a surrounding membrane as the polar nucleus (pl. 16, fig. 6). In such megagametophytes the cytoplasm becomes crowded towards the upper part of the embryo sac, finally becoming quite dense. The degree of density as revealed by appropriate stain technique is often a good indication of approaching sterility of that particular ovule. In normally constituted megagametophytes the synergids are well constructed, each with a prominent indentation and filiform apparatus (pl. 16, fig. 5).

After the first division in the functioning megaspore, there occurs a sudden and rapid growth of the embryo sac and the nucellus is extensively ravaged in the region of the egg cell, thus giving the median longitudinal section of the sac a sagittate outline.

## FERTILIZATION

The time elapsing between pollination and fertilization is apparently rather long. This point was not realized at the time the material was collected, and it is not now possible to study the problem experimentally

without procuring more plants. In one collection of ovaries which was marked for 'zygotes,' no sign of the microgametophyte could be seen in the 40-odd ovaries sectioned. In a collection presumed to show early stages in embryogenesis, fertilization was just commencing; by sectioning material of the latest stages collected, it was found that the embryo completes cotyledon development after the ovary has become detached from the stem, consequently it will be seen that little dependence can be placed upon the condition of the flowers to show what is happening within the ovary. In a later paper, I shall show that this is particularly the case in *Burragea*. In *Stenosiphon* the time required for the microgametophyte to reach the megagametophyte is computed as being at least 72 hours, and may be even longer. Does this long period permit a selective action with regard to the ovule to be fertilized?

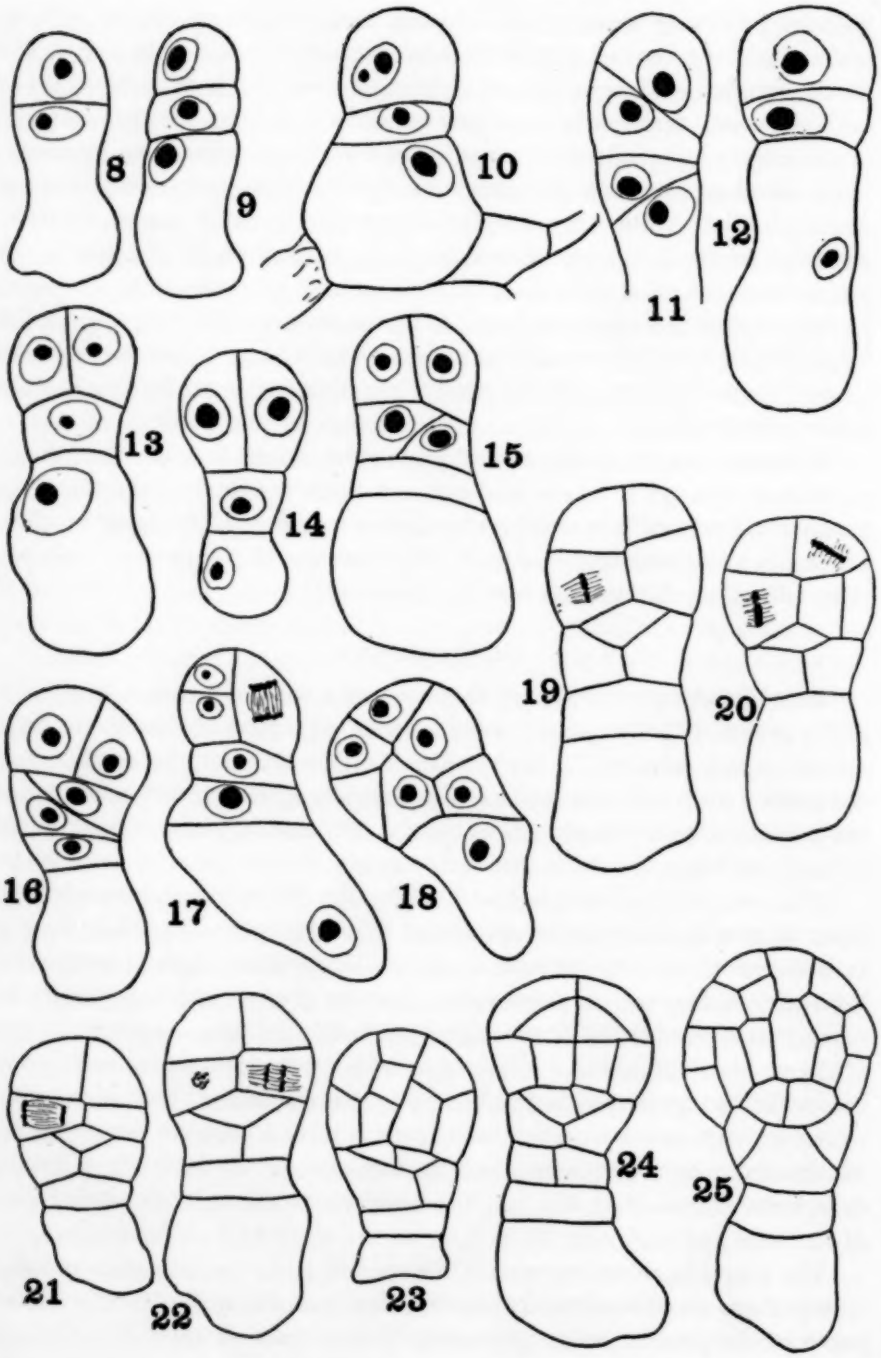
Syngamy was studied in several preparations, but details were difficult to observe clearly; it was considered not worth while to make the large number of preparations required for a thorough study of this topic. The process in any event seems normal. The union of the secondary male nucleus with the polar nucleus was not observed.

## EMBRYOGENESIS

Immediately after syngamy there occurs a sudden increase in the size of the zygote, but this growth is just as suddenly checked shortly after the second zygotic mitosis. As the number of cells multiplies, the embryo does not make a proportionate increase in total bulk, gaining in size over that of the 2-celled stage by barely 10 per cent at the time cotyledon development is ready to begin.

The young embryo is attached firmly to the thick micropylar peripheral layer of megagametophytic cytoplasm (text fig. 10), occasionally being turned over to one side, or even dragged slightly down the side of the embryo sac. When such a phenomenon occurs, the embryo is generally irregular (text fig. 18), hence we might conclude that the proper orientation of the embryo within the ovule (i.e., in a line with the longitudinal axis of the ovule) is a prerequisite to absence of abnormalities. The relation between gravity and orientation of the embryo is a problem requiring investigation. As a consequence of the attachment of the embryo to the cytoplasm surrounding the sac, the basal suspensor cell is rather broad at the base and may even be as large as the remainder of the embryo.

The stages in embryogenesis in the species under consideration parallel closely those considered typical for the family and described in the second paper of the present series (Johansen, 1930). Immediately after the primary transverse division there occurs a second transverse partitioning in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the innermost cell (text fig. 9), so that a three-celled stage occurs before there is a longitudinal sectioning of the uppermost cell. A fourth transverse wall is rarely seen, this probably resulting from an abnormal mitosis (text fig. 11). The quadrant and succeeding stages are typical in all respects (text figs. 13–25).

The hypophysis cell divides at an early period, usually immediately after the embryo proper has attained the octant stage (text fig. 19). Almost as soon as the wall, concave from above and characteristic of the family, is fully completed, a vertical wall is established in the lower daughter cell. This wall appears considerably earlier than in other species of the Onagraceae.

Simultaneous mitoses in two or more cells of a young embryo occur rarely among dicotyledons, as far as a perusal of the literature and my own observations go. *Stenosiphon* is apparently an exception, as mitoses were noticed with great frequency (e.g., text figs. 19–22). Growth in the embryo of this plant is most active just before noon; no mitoses were observed in material collected between 1:00 p. m. and 11:30 p. m.

As in other species, there may occasionally be an irregularly formed wall in the hypophysis cell (text figs. 15, 16). I could not find that this exerts any untoward effect on the future growth of the embryo. The embryo of *Stenosiphon*, in fact, is characterized by the absence of the irregularities which are so prevalent in other onagrads.

As noted earlier, the ovaries drop off the stems while still green and immature. Growth of the embryo proceeds even after the ovaries have dropped, and this fact was unfortunately not known while the plants were growing. Cotyledon development evidently begins after the ovaries have dropped, because the oldest stage I could find in the material available, pictured in text figure 25, is too early to show clearly the commencement of cotyledon growth. It may, however, be reasonably concluded that the cotyledons develop in the typical manner, because a fairly high germination percentage of the seeds can be secured and the seedlings are perfectly normal.

Embryos of parthenogenetic or apogamic origin were not encountered. The prevalence of these phenomena in other onagrads (*Zauschneria*,

Figs. 8–25. Embryogenesis. All figures ×320. Fig. 8. Two-celled embryo. 9. Three-celled embryo. 10. Same, showing attachment to peripheral layer of megagametophytic (=endosperm) cytoplasm by broad-based suspensor cell. 11. Oblique dividing walls in four-celled embryo. 12. Rather large three-celled stage. 13, 14. Quadrant stages. (In describing quadrant and octant stages, the hypophysis and suspensor cells are not counted.) 15, 16. Unequal, premature division of hypophysis cell. 17. Octant stage. 18. Irregular embryo drawn halfway down side of embryo sac. 19. Divisions in hypophysis cell complete. 20–25. Later stages, all normal.

*Taraxia*, *Godetia*, etc.) causes one to wonder why the egg cell in any of the three non-fertilized ovules cannot similarly develop into an embryo-like structure. The preparations show quite plainly that once one of the ovules is fertilized, the death and disintegration of the other three is at the same time, in some unknown manner, very definitely decreed.

## THE ENDOSPERM

Fusion of the polar nucleus with the secondary male nucleus, as well as the first mitosis of the endosperm nucleus so constituted, are evidently very rapid processes, as neither was observed. The endosperm nuclei are at first large and concentrated at the chalazal end of the sac. The total number of nuclei produced is very small, there being but few mitoses, and the entire mass of cytoplasm and nuclei has disappeared by the time the embryo has reached the 128-celled stage. Although every one of the more than 150 ovules containing embryos were carefully searched, no endosperm mitoses were found. False cell formation, as described for *Taraxia ovata* (Johansen, 1931), does not occur.

## CONCLUSIONS

1. The young ovary is 4-loculate, each locule containing a single ovule; the fruit is one-celled and one-seeded, because

2. Only one ovule is ever fertilized, the three remaining ovules always perishing.

3. The funiculus of each ovule is surmounted by a dense tuft of hairs, which guide the single microgametophyte to the micropyle.

4. No reliable criterion as to which ovule is to be fertilized can be assigned.

5. Megagametogenesis follows the scheme typical for the family, but organization is not always perfect.

6. Embryogenesis is normal and characterized by the absence of irregularities. The development of the cotyledons progresses after the ovary, still green and immature, drops from the stem.

7. The morphological evidence shows that the position assigned *Stenosiphon* in my phylogenetic scheme (Johansen, 1929b) is justified.

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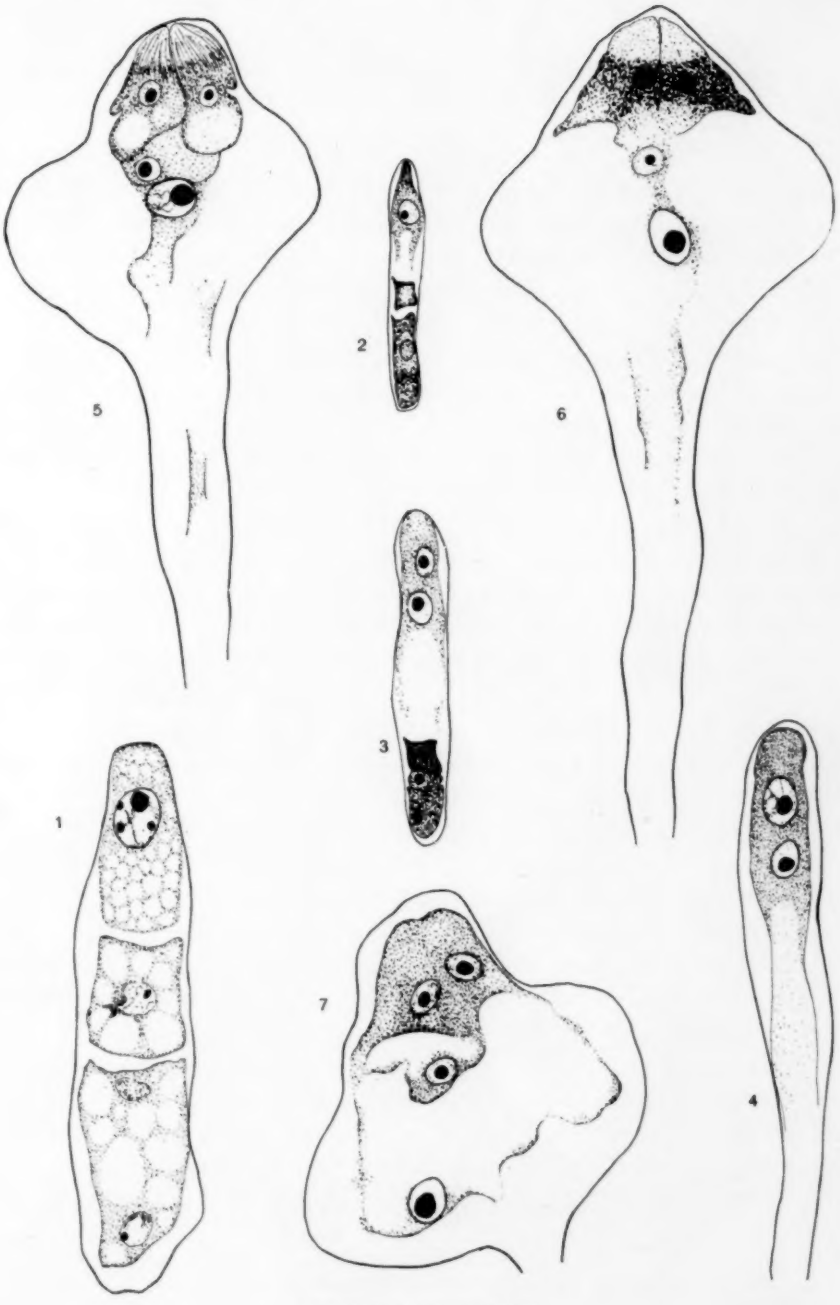
## Description of plate 16

All figures ×475.

Fig. 1. Quartet in which no cell wall was formed in lower secondary megasporocyte following homotypic mitosis.
Fig. 2. Functioning megaspore.
Figs. 3, 4. Binucleate megagametophytes.
Fig. 5. Normal megagametophyte.
Fig. 6. Megagametophyte with naked egg cell and poorly developed synergids.
Fig. 7. Synergids unorganized and egg cell partially bounded by cytoplasmic membrane.




JOHANSEN: STENOSIPHON

UNIV. OF MICH.

# The seed-plants and ferns of the Glacier Bay National Monument, Alaska

WILLIAM S. COOPER

In 1923 the Ecological Society of America initiated a campaign to have the region surrounding Glacier Bay, Alaska, set aside as a National Monument. The movement reached a successful issue when President Coolidge, in 1925, issued a proclamation establishing such a reservation. The features justifying this action were both scenic and scientific. In the first class are the lofty mountains, culminating in Mt. Fairweather (15,300 ft.), and the great tidal ice-fronts of the glaciers. Scientifically the region offers unrivaled opportunities for the study of glacial geology and the behavior of plants and animals in relation to glacier advance and retreat.

My own acquaintance with Glacier Bay began in 1916, in a brief expedition which was intended to be the first in a long-period study of the establishment of vegetation following glacier retreat. Two other visits have been made, in 1921 and 1929, and it is hoped to continue the series at approximately five-year intervals. The ecological results of the first two expeditions have been presented in a former paper,[1] two others,[2] are based upon the expedition of 1929.

As a necessary concomitant to the ecological work, seed-plants, ferns, mosses and lichens were collected in as thorough a way as was possible. The materials are now sufficiently abundant to justify the publication of an annotated list of the first two classes; adequate treatment of mosses and lichens must await a visit by specialists in those groups.

The list is, of course, far from complete, and the distribution of the species within the area explored is of necessity inadequately indicated. Unquestionably many species have been overlooked, but exploration has been sufficiently thorough to justify the assumption that most of those missed are of rare occurrence. I feel that the catalogue in a general way gives a true picture of the plant population.

The flora of the Glacier Bay region is not an extensive one—an interesting fact in itself, considered in connection with the history of the region. About one hundred and fifty years ago the entire bay was occupied by a great trunk glacier fed by many tributaries with sources in the surrounding mountains. In the last century and a half this immense body of

[1] The recent ecological history of Glacier Bay, Alaska. Ecology **4**: 93–128, 223–246, 355–365. 1923.

[2] A third ecological expedition to Glacier Bay, Alaska. Ecology **12**:61–95. 1931.

The layering habit in Sitka spruce and the two western hemlocks. Botanical Gazette.

ice, sixty miles long, has disappeared completely. Its former tributaries survive as separate ice streams, some reaching the bay, others stopping short of it. The plant population is thus the product of a very recent invasion, and the list of today, even if complete, would fall far short of the number of species that could, and in the future will with sufficient time, migrate into the region. An interesting list might be compiled of common plants of southeastern Alaska which apparently have not yet entered the newly exposed area.

One portion of the region has not yet been visited: the upper mountain slopes of the lower bay, above the limit of the last glacial advance. This would yield many additional species, which, however, would be of merely incidental interest for the present purpose, since the accompanying list is strictly an attempt to cover the flora of the area left bare by the retreat of the ice following its maximum of a hundred and fifty years ago. In carrying out this purpose it is necessary to transgress the southern boundary of the National Monument, for the lower bay is not included in the reservation. It is also logical to cover a large portion of the foreland east of the lower bay which was not actually invaded by the ice, but which received at the same time a thick mantle of sterile outwash materials.

A brief characterization of the communities and successional features of the region will be of interest. Upon smooth glaciated rocks we find crevice pioneers, which, with mosses and lichens, produce in time a complete mat of vegetation, the process here being naturally a slow one. Upon fresh moraine and outwash, invasion and successional progress are rapid. The complete list of pioneers is a long one, but only a few are of real importance: *Equisetum variegatum*, *Epilobium latifolium*, *Dryas Drummondii*, and the prostrate willows. In areas of wet gravels and along watercourses we find especially fruitful collecting grounds. Amelioration of the habitat makes possible the establishment of the thicket stage, which at first is open, the smaller bushy willows such as *Salix Barclayi* and *S. commutata* predominating. Many of the pioneers still maintain themselves, and a new group of herbs enters with the scattered shrubs. As *Salix sitchensis*, *S. alaxensis* and *Alnus tenuifolia* attain their full growth, the thicket becomes closed and rather dense shade develops. The pioneers disappear completely and the herbage becomes rank and varied, tall ferns, including *Athyrium filix-foemina*, *Dryopteris dilatata*, *Adiantum pedatum* var. *aleuticum*, and *Polystichum Andersoni*, being conspicuous. Most of the few species that characterize the forest stage first appear in the closed thicket. The thicket stage thus presents the longest and most varied list of the whole successional series. In the spruce forest which follows, seed plants are few in species and sparse in distribution, the great bulk of the lower growth being

made up of mosses. Nowhere within the recently glaciated area has the mature climax become established; the spruce, the first of the conifers to attain dominance, forms nearly pure stands. The final process, the increase in importance of the two hemlocks, is, however, well under way. The boundary between the young spruce forest of the recently glaciated region and the mature spruce-hemlock climax of the adjoining areas is an exceedingly sharp one. The earlier stages, too, are very definitely spaced: the spruce forest occupies the shores of the lower bay, the thicket clothes the slopes of the middle portion, and the upper reaches, most recently vacated by the ice, are in part occupied by the pioneer community and in part entirely bare.

Two other habitats should be mentioned: the morainic and rock basin ponds and lakes, which, even in pioneer localities, support a small population of aquatics; and the tidal shores, where a very evident division into zones is apparent.

In the annotations I have aimed to give, wherever possible, the characteristic habitat and community preferences of the species and its successional rôle. In many instances, where but one or two occurrences were noted, adequate ecological characterization is impossible. Since the area is an extensive one, references are given, in the case of the less frequent species, to the stations where collections were made. A map furnishing the key to these may be found in Ecology **12**: 62. *fig. 1.*

The main body of the collection has been determined by Mr. Paul C. Standley, of the Field Museum of Natural History, Chicago. Certain groups have been referred to specialists: Mrs. Agnes Chase has examined most of the grasses, and Mr. K. K. Mackenzie the sedges. Dr. C. R. Ball determined the willows collected in 1916, and Dr. W. R. Maxon the ferns of the 1921 expedition. The names of these specialists have been attached in the list to the species which they have examined; if no name is given, Mr. Standley has made the determination. Mr. Standley has also furnished a list of species obtained at Glacier Bay by other visitors, and not seen by me. These are included here, the name of the collector being added in each case. Sets of the collections made in 1916 and 1921 have been deposited in the herbarium of the United States National Museum in Washington; sets of the 1929 collection are to be found in the herbaria of the Field Museum of Natural History, Oberlin College, and the University of Minnesota.

It is a pleasure to acknowledge the cooperation of Miss Frances E. Andrews, of Minneapolis, in the collecting done in 1929. Mr. Chester Roys, of Moline, Illinois, also gave valuable assistance in that year, and Mrs. Cooper in 1921 and 1929.

## OPHIOGLOSSACEAE

Botrychium vulgare (L.) Sw. In a variety of meadow communities.

## POLYPODIACEAE

ADIANTUM PEDATUM ALEUTICUM Rupr. Closed thicket (48); sheltered rock crevice in pioneer locality (27).

ASPLENIUM VIRIDE Huds. Rock crevice (39).

ATHYRIUM FILIX-FOEMINA (L.) Roth. Closed thicket, abundant, persisting into spruce forest, occasionally pioneer in sheltered rock crevices (27, 42).

CRYPTOGRAMMA ACROSTICHOIDES R. Br. Pioneer in rock crevices.

CYSTOPTERIS FRAGILIS (L.) Bernh. Pioneer in rock crevices, persisting into thicket and forest stages.

DRYOPTERIS DILATATA (Hoffm.) Gray. Abundant in closed thicket, persisting into spruce forest.

DRYOPTERIS LINNAEANA C. Chr. Characteristic of spruce forest, but appearing in the thicket stage and occasionally as a rock crevice pioneer. Maxon.

POLYPODIUM VULGARE L. On rocks in spruce forest. F. K. Butters.

POLYSTICHUM ANDERSONI Hopkins. Closed thicket. The handsomest fern of the region. First reported from Alaska by the writer in 1921 (Tracy Arm, Holkham Bay); found at Glacier Bay in 1929 (48).

POLYSTICHUM BRAUNII (Spenn.) Fée. Closed thicket (11), persisting into spruce forest (5). Maxon.

POLYSTICHUM LONCHITIS (L.) Roth. Pioneer in sheltered rock crevices (27), persisting into closed thicket stage (48).

## EQUISETACEAE

EQUISETUM ARVENSE L. Common as a pioneer on wet or saturated glacial deposits, especially silt. Persisting into closed thicket, where it makes an abundant and rank growth.

EQUISETUM HYEMALE ROBUSTUM (A. Br. ) A. A. Eaton.

EQUISETUM SCIRPOIDES Michx. Wet bank at a single pioneer locality (19). Cooper.

EQUISETUM VARIEGATUM Schleich. Omnipresent pioneer on moraine, gravel and silt, also invading the margins of newly formed morainic ponds and rock pools.

## LYCOPODIACEAE

LYCOPODIUM ALPINUM L. Open thicket (2).

LYCOPODIUM ANNOTINUM L. Spruce forest.

LYCOPODIUM SELAGO L. Thicket (22). Cooper.

LYCOPODIUM SITCHENSE Rupr. Open spruce forest (53).

## CONIFERAE

PICEA SITCHENSIS Carr. The dominant species in the young forest that covers the foreland and lower mountain slopes of the lower bay. Here it forms dense, nearly pure stands, the largest trees being about two feet in diameter. It occasionally enters as a pioneer on moraine and gravels, and more and more frequently as the succession advances, so that the closed thicket always has frequent spruces rising above the general level. It layers abundantly in open localities.[3] Cooper.

[3] Botanical Gazette. In press.

PINUS CONTORTA Dougl. Very rare in the Glacier Bay region, isolated individuals being found here and there in pioneer localities and in swales in the spruce forest. It is more abundant on the outwash flat east of the mouth of the bay, here apparently forming an incomplete successional stage antecedent to the spruce. Cooper.

TSUGA HETEROPHYLLA Sarg. Young individuals occur frequently in the spruce forests of the lower bay. Its establishment in abundance (with the next species) will mark the complete attainment of the regional climax. It is found very occasionally in pioneer localities and infrequently in the thicket. Cooper.

TSUGA MERTENSIANA Carr. Like the last in occurrence and successional rôle. Cooper.

## NAJADACEAE

POTAMOGETON FILIFORMIS L. Morainic ponds and lakes (41, 44).

## JUNCAGINACEAE

TRIGLOCHIN MARITIMA L. Inter-tidal zone of shores (3, 53). Cooper.

## GRAMINEAE

AGROPYRON TENERUM Vasey. Pioneer on gravel (12).

AGROPYRON VIOLACEUM (Hornem.) Lange. Beach meadow (26, 53). Chase.

AGROSTIS HIEMALIS GEMINATA (Trin.) Hitchc. Pioneer on wet gravel, in various meadow communities. Chase.

AIRA CAESPITOSA L. Meadow communities. Chase.

CALAMAGROSTIS NEGLECTA (Ehrh.) Gaertn. Station 26. Chase.

CALAMAGROSTIS SCABRA Presl. Meadow communities (52). Chase.

ELYMUS ARENARIUS L. Beach above high tide limit, forming a fairly continuous zone along the shores of the lower bay, and established in occasional spots in pioneer localities of the upper bay (25, 26). Cooper.

FESTUCA RUBRA L. Pioneer on wet gravel and common in meadow habitats.

HORDEUM BOREALE Scribn. and Smith. Pioneer on wet gravel and along shores. Chase.

PHLEUM ALPINUM L. Wet gravel pioneer; beach meadow.

POA ALPINA L. Frequent pioneer on moraine and gravels and in rock crevices. Cooper.

POA ANNUA L. Occasional in a variety of habitats.

POA ARCTICA R. Br. Wet gravel, rock crevices. At 22 abundantly proliferous. The habit is apparently frequent in this species, having been reported also by Lutz (Ecology 11: 564). Chase.

POA EMINENS Trin.

POA GRACILLIMA Vasey. Pioneer on wet gravel (14, 18).

POA HISPIDULA Vasey. Rock crevice (39).

POA LAXA Haenke. Rock crevice (39).

POA PRATENSIS L. Frequent in various meadow communities. Chase.

POA STENANTHA Trin. Station 44. Chase.

PUCCINELLIA MARITIMA (Huds.) Parl. Inter-tidal zone of shores (3).

PUCCINELLIA PAUPERCULA ALASKANA (Scribn. and Merr.) Fern. and Weath. Common in inter-tidal zone of shores; in upper bay at 26. Chase.

PUCCINELLIA PHRYGANODES (Trin.) S. and M. Inter-tidal zone of shores (3).

TORRESIA ODORATA (L.) Hitchc. Beach meadow (53) and open thicket (52). Cooper.

TRISETUM SPICATUM (L.) Richter. Common pioneer on gravel and moraine and in rock crevices.

## CYPERACEAE

CAREX CAPILLARIS L. Pioneer localities (27). Mackenzie.
CAREX CRYPTOCARPA Mey. Shore (3).
CAREX HASSEI Bailey. Pioneer localities (27). Mackenzie.
CAREX HEPBURNII Boott. Mackenzie.
CAREX INCURVA Lightf. Pioneer on wet gravel (26, 27, 44). Mackenzie.
CAREX LYNGBYEI Hornem. Beach meadow (6). Mackenzie.
CAREX MACROCHAETA C. A. Meyer. Open thicket (49). Mackenzie.
CAREX PHAEOCEPHALA Piper. Pioneer localities (25, 27). Mackenzie.
CAREX VULGARIS Fries. Edge of rock basin pond (27).
ELEOCHARIS PALUSTRIS (L.) R. and S. Margin of pond (4).
ERIOPHORUM SCHEUCHZERI Hoppe. Edge of morainic pond (14).
SCIRPUS CAESPITOSUS L.

## JUNCACEAE

JUNCUS ALPINUS Vill. Pioneer localities (27).
JUNCUS BALTICUS Willd. Pioneer localities (27).
JUNCUS CASTANEUS Sm. Wet gravel. Station 44.
JUNCUS HAENKEI E. Mey. Common pioneer on wet gravel and margins of morainic ponds.
JUNCUS MERTENSIANUS Bong. Pioneer localities (27).
JUNCUS TRIGLUMIS L. Shore (6).
LUZULA CAMPESTRIS (L.) DC. Frequent pioneer on gravel and moraine.

## LILIACEAE

FRITILLARIA CAMTSCHATCENSIS (L.) Gawler. Beach meadow: frequent along shores of lower bay.
STREPTOPUS AMPLEXIFOLIUS (L.) DC. Closed thicket, persisting into spruce forest. Cooper.
TOFIELDIA INTERMEDIA Rydb. Wet gravel and beach meadow.

## ORCHIDACEAE

CORALLORHIZA MERTENSIANA Bong. Closed thicket (22).
CYPRIPEDIUM MONTANUM Dougl. Closed thicket (22). First record for Alaska. The species was found also, in 1929, on the Stikine River, near the mouth of the Clearwater, a short distance east of the Alaska boundary. The Glacier Bay occurrence is remarkable in that a species presumably slow in migration was found far from other recorded localities in a spot vacated by the ice not more than a century ago.
HABENARIA BRACTEATA (Willd.) R. Br. Beach meadow and open thicket (1, 4, 49).
HABENARIA DILATATA (Pursh) Hook. Rock pioneer (16); moraine meadow (52).
HABENARIA HYPERBOREA (L.) R. Br. Frequent pioneer on moraine and gravel.
HABENARIA LEUCOSTACHYS (Lindl.) Wats. Beach meadow (6).
MALAXIS DIPHYLLOS Cham. Station 5.
OPHRYS CORDATA L. Common in spruce forest.
SPIRANTHES ROMANZOFFIANA Cham. Frequent pioneer on wet gravel, and in beach meadow and open thicket.

## SALICACEAE

POPULUS TRICHOCARPA T. and G. Frequent pioneer on moraine and gravels, common in the closed thicket, standing conspicuously above the willows and alders, gradually disappearing as the climax gains control.

SALIX ALAXENSIS (And.) Coville. One of the dominants of the closed thicket stage. Ball.

SALIX ARCTICA Pall. The most important of the prostrate willows both in abundance and bulk: a common pioneer on moraine and gravels, persisting into the open thicket stage. Ball.

SALIX BARCLAYI Anders. Very common in pioneer and semi-pioneer localities, tending to supersede the prostrate willows and being superseded in turn by *S. alaxensis* and *S. sitchensis*. Ball.

SALIX BEBBIANA Sarg. Delta flat at Beartrack Cove (6).

SALIX COMMUTATA Bebb. Common with *S. Barclayi;* more successful than that species in maintaining itself in competition with *S. alaxensis* and *S. sitchensis*. Ball.

SALIX COMMUTATA DENUDATA Bebb. Station 10. Ball.

SALIX GLAUCA L. Frequent with *S. Barclayi*. Ball.

SALIX RETICULATA L. Frequent pioneer with *S. arctica*, persisting into the open thicket stage. Ball.

SALIX SCOULERIANA Barratt. Station 18.

SALIX SITCHENSIS Bong. With *S. alaxensis* and *Alnus tenuifolia* dominating the closed thicket, entering as an early pioneer. Cooper.

SALIX STOLONIFERA Coville. A frequent pioneer with *S. arctica*, persisting into the open thicket. Ball.

## BETULACEAE

ALNUS TENUIFOLIA Nutt. With *Salix alaxensis* and *S. sitchensis* dominating the closed thicket. Individuals starting at widely separated points in pioneer territory serve as centers of rapid aggregation.

## URTICACEAE

URTICA LYALLII Wats. Station 9.

## POLYGONACEAE

OXYRIA DIGYNA (L.) Camptdera. Frequent pioneer in rock crevices. Cooper.

POLYGONUM FOWLERI Rob. Shore (14).

POLYGONUM VIVIPARUM L. Pioneer on wet gravel; various meadow habitats. Cooper.

## CHENOPODIACEAE

ATRIPLEX ALASKENSIS Wats. Inter-tidal zone of shores, with *Plantago maritima*.

ATRIPLEX GMELINI Mey. Shore (51).

## CARYOPHYLLACEAE

HONKENYA PEPLOIDES OBLONGIFOLIA (T. and G.) Wight. Shores at high tide limit, just below *Elymus arenarius*.

MOEHRINGIA LATERIFLORA (L.) Fenzl. Beach meadow, open thicket.

SAGINA SAGINOIDES (L.) Britton. Frequent pioneer on moraine and gravels.

SILENE ACAULIS L. Frequent pioneer on moraine and gravels.
SPERGULARIA MARITIMA (L.) Griseb. Inter-tidal zone of shores.
STELLARIA BOREALIS Bigel. Open thicket (25); spruce forest (5).
STELLARIA CRISPA C. and S. Shore (3).
STELLARIA LONGIPES Goldie. Pioneer (27); open thicket (25).

## RANUNCULACEAE

ACTAEA ARGUTA Nutt. Closed thicket (9, 51), persisting into spruce forest (5). Cooper.
ANEMONE HUDSONIANA (DC) Richards. Point Gustavus, Coville and Kearney.
ANEMONE PARVIFLORA Michx. Hooniah village, Coville and Kearney.
CALTHA PALUSTRIS ASARIFOLIA (DC) Huth. Marshy spot in thicket (51). Point Gustavus, Coville and Kearney.
RANUNCULUS BONGARDI Greene. Edge of closed thicket (48).
RANUNCULUS ESCHSCHOLTZII Schlecht. Muir Inlet and Point Gustavus, Coville and Kearney.
RANUNCULUS HYPERBOREUS Rottb. Coville and Kearney.

## CRUCIFERAE

ARABIS AMBIGUA DC. Pioneer on moraine and gravels, persisting into open thicket stage.
ARABIS HIRSUTA (L.) Scop. Open thicket (49).
COCHLEARIA OBLONGIFOLIA DC. Shores.
RORIPA CLAVATA Rydb. Shores.

## CRASSULACEAE

SEDUM INTEGRIFOLIUM (Raf.) Nels. Pioneer on wet gravel; rock crevices (26, 39).

## SAXIFRAGACEAE

HEUCHERA GLABRA Willd. Rock crevices (39) and meadows.
LEPTARRHENA PYROLIFOLIA (Don) R. Br. Point Gustavus, Coville and Kearney.
PARNASSIA KOTZEBUEI Cham. Pioneer on wet gravel.
PARNASSIA PALUSTRIS L. Pioneer on wet gravel; moist meadows.
RIBES BRACTEOSUM Dougl. Station 5. Cooper.
RIBES LACUSTRE (Pers.) Poir. Hooniah village, Coville and Kearney.
RIBES LAXIFLORUM Pursh. Closed thicket, persisting into spruce forest.
SAXIFRAGA ADSCENDENS L. Station 39.
SAXIFRAGA CAESPITOSA L. Open thicket (39, 49).
SAXIFRAGA LYALLII Engler. Russell Island (27).
SAXIFRAGA NIVALIS L. Rock pioneer.
SAXIFRAGA OPPOSITIFOLIA L. Frequent pioneer on moraine and gravels. Cooper.
SAXIFRAGA TRICUSPIDATA Rottb. Rock crevices, persisting into thicket stage.
TIARELLA TRIFOLIATA L. Hooniah, Walker.

## ROSACEAE

ARUNCUS VULGARIS Raf. Closed thicket (9), persisting into spruce forest (8).
DRYAS DRUMMONDII Rich. The most important pioneer on moraine and gravels, persisting into the open thicket stage. Cooper.

DRYAS INTEGRIFOLIA Vahl. Occasional pioneer on moraine and gravels (27).
DRYAS OCTOPETALA L. Occasional pioneer on moraine and gravels (27), persisting into the open thicket stage (49).
FRAGARIA CHILOENSIS (L.) Duch. Abundant in beach meadow along shores of lower bay, invading zone of *Elymus;* also common in open thicket. Found in upper bay at 25. Cooper.
GEUM MACROPHYLLUM Willd. Open and closed thicket (9, 49, 51).
POTENTILLA ANSERINA L. Shores, below *Elymus* zone (6, 10, 26).
POTENTILLA VILLOSA Pall. Open thicket (39); beach meadow (53).
RUBUS ARCTICUS L. Hooniah, Walker.
RUBUS CHAMAEMORUS L. Closed thicket (22); beach meadow (9).
RUBUS PEDATUS J. E. Sm. Glacier Bay, Walker.
RUBUS SPECTABILIS Pursh. Common in closed thicket, persisting into spruce forest. Cooper.
RUBUS STELLATUS Sm. Closed thicket and spruce forest, common.
SANGUISORBA SITCHENSIS C. A. Meyer. Beach meadow; open and closed thicket.
SIBBALDIA PROCUMBENS L. Pioneer in rock crevices and on moraine and gravels.
SORBUS SITCHENSIS Roem. Muir Inlet, Coville and Kearney.

## LEGUMINOSAE

ASTRAGALUS ALPINUS L. Pioneer on moraine and gravels, becoming common in the open thicket stage.
HEDYSARUM AMERICANUM (Michx.) Britton. Pioneer on wet gravel, persisting into the open thicket stage.
LATHYRUS MARITIMUS Bigel. Top of beach, shores of lower bay. Cooper.
LUPINUS NOOTKATENSIS Don. Various meadow communities, lower bay.
OXYTROPIS CAMPESTRIS (L.) DC. Pioneer on wet gravel; open thicket.
OXYTROPIS GRACILIS A. Nels. Rocky island (22).

## CALLITRICHACEAE

CALLITRICHE PALUSTRIS L.

## EMPETRACEAE

EMPETRUM NIGRUM L. Pioneer on moraine and gravels, becoming common in open thicket. Cooper.

## ELAEAGNACEAE

SHEPHERDIA CANADENSIS (L.) Nutt. Occasional pioneer on moraine and gravels, becoming frequent in open thicket.

## ONAGRACEAE

EPILOBIUM ADENOCAULON Hausskn.
EPILOBIUM ANAGALLIDIFOLIUM Lam. Pioneer on wet gravel; sheltered rock crevices.
EPILOBIUM ANGUSTIFOLIUM L. Various meadow communities; open thicket. Cooper.
EPILOBIUM BEHRINGIANUM Hausskn. Muir Glacier, Trelease and Saunders.
EPILOBIUM BONGARDI Hausskn. Open thicket (49).
EPILOBIUM LATIFOLIUM L. This and *Equisetum variegatum* are the first conspicuous

pioneers on gravel and moraine; both vary in luxuriance directly with the moistness of the habitat. Cooper.

EPILOBIUM LEPTOCARPUM Hausskn. Shore (14).

## HALORAGIDACEAE

HIPPURIS VULGARIS L. Morainic ponds (52).

MYRIOPHYLLUM SPICATUM L. Morainic ponds (4, 52).

## UMBELLIFERAE

ANGELICA GENUFLEXA Nutt. Beach meadow (53).

COELOPLEURUM GMELINI (DC.) Ledeb. Point Gustavus, Coville and Kearney.

CONIOSELINUM GMELINI (C. and S.) C. and R. Various meadow and thicket communities (9, 51).

HERACLEUM LANATUM Michx. Beach meadow and thicket, lower bay. Cooper.

LIGUSTICUM SCOTHICUM L. Beach meadow.

OSMORHIZA DIVARICATA Nutt. Edge of thicket (48).

OSMORHIZA PURPUREA (C. and R.) Suksd. Point Gustavus, Coville and Kearney.

## ARALIACEAE

FATSIA HORRIDA (Sm.) B. and H. Closed thicket and spruce forest, lower bay (8, 51). Cooper.

## ERICACEAE

ARCTOSTAPHYLOS UVA-URSI Spreng. Rock pioneer; beach meadow; open thicket. Cooper.

ARCTOUS ALPINA (L.) Niedenzu. Occasional pioneer on moraine and gravels, persisting into open thicket stage.

MENZIESIA FERRUGINEA Smith. Spruce forest, lower bay (8, 52). Cooper.

MONESES UNIFLORA (L.) Gray. Closed thicket (22); common in spruce forest, lower bay (5, 50). Cooper.

PHYLLODOCE GLANDULIFLORA (Hook.) Coville. Open thicket (23, 37). Cooper.

PYROLA CHLORANTHA Sw. Spruce forest (8); first record for Alaska.

PYROLA SECUNDA L. Characteristic of the later successional stages — closed thicket and spruce forest; found also with considerable frequency in a variety of more primitive habitats: as a pioneer on rock, moraine and gravels, in beach meadow and open thicket.

PYROLA ULIGINOSA T. and G. Open thicket, becoming common in closed thicket, persisting into spruce forest.

VACCINIUM OVALIFOLIUM Sm. Muir Inlet, Coville and Kearney.

VACCINIUM ULIGINOSUM L. Infrequent pioneer on moraine and gravels (27); frequent in open thicket (37, 49).

## PRIMULACEAE

DODECATHEON PAUCIFLORUM (Durand) Greene. Beach meadow, lower bay (1, 6, 53).

GLAUX MARITIMA L. Inter-tidal zone of shores, with *Plantago maritima* (53). Cooper.

PRIMULA EGALIKSENSIS Wormskj. Glacier Bay, Coville and Kearney.

## GENTIANACEAE

GENTIANA ACUTA Michx. Beach meadow (53).

GENTIANA PROPINQUA Richards. Glacier Bay, Stephens.

LOMATOGONIUM ROTATUM (L.) Fries. Beach meadow, extending downward into *Plantago* zone. (3, 6, 53).

MENYANTHES TRIFOLIATA L. Moraine pond (2). Cooper.

## HYDROPHYLLACEAE

ROMANZOFFIA SITCHENSIS Bong. Moist rock crevices (25).

## BORAGINACEAE

PNEUMARIA MARITIMA (L.) Hill. Shingle beaches, just above high tide limit; found in upper bay at 25 and 26.

## LABIATAE

PRUNELLA VULGARIS L. Silty shore (6).

## SCROPHULARIACEAE

CASTILLEJA LANCIFOLIA Rydb. Beach meadow (41, 49).

CASTILLEJA LUTESCENS (Greenm.) Rydb. Hooniah, Walker.

CASTILLEJA MINIATA Dougl. Beach meadow (1).

CASTILLEJA PALLIDA (L.) Kunth. Beach meadow (1); thicket (22).

CASTILLEJA RHEXIFOLIA Rydb. Station 41.

EUPHRASIA MOLLIS (Ledeb.) Wettst. Scattered but omnipresent pioneer on moraine and gravels, persisting into open thicket stage.

RHINANTHUS CRISTA-GALLI L. Various moist open localities: wet gravel, beach meadow, moraine meadow. Cooper.

VERONICA AMERICANA Schw. Hooniah, Walker.

## OROBANCHACEAE

BOSCHNIAKIA ROSSICA (C. and S.) Standley. Closed thicket, lower bay (5, 11).

## LENTIBULARIACEAE

PINGUICULA VULGARIS L. Wet gravels and wet beach meadows. Cooper.

## PLANTAGINACEAE

PLANTAGO MARITIMA L. Inter-tidal zone of shores, mainly lower bay; in upper bay found at 26. Cooper.

## RUBIACEAE

GALIUM TRIFIDUM L. Station 52.

GALIUM TRIFLORUM Michx. Beach meadow and thicket (9).

## CAPRIFOLIACEAE

SAMBUCUS PUBENS Michx. Closed thicket, persisting into spruce forest, lower bay. Cooper.

VIBURNUM PAUCIFLORUM Pylaie. Young spruce forest (53). Cooper.

## VALERIANACEAE

VALERIANA SITCHENSIS Bong. Spruce forest (5).

## CAMPANULACEAE

CAMPANULA ALASKANA (Gray) Wight. Beach meadow; moraine meadow; open thicket.

## COMPOSITAE

ACHILLEA BOREALIS Bong. In various open communities: most characteristic of the beach meadow; also in open thicket and as a pioneer on gravel. Cooper.

ANAPHALIS MARGARITACEA (L.) B. and H. Occasional pioneer on moraine and gravels, persisting into open thicket stage.

ANTENNARIA BOREALIS Greene. Pioneer on moraine and gravels, persisting into open thicket stage.

ANTENNARIA MONOCEPHALA DC.

ANTENNARIA PALLIDA E. Nels. Open thicket (4).

ARNICA CHAMISSONIS Less. Open thicket (4).

ARNICA OBTUSIFOLIA Less. Open thicket (49).

ASTER SUBSPICATUS Nees. Moraine meadow (52).

CREPIS NANA Richards. Occasional pioneer on moraine and gravels (26, 27).

ERIGERON ACRIS L. Occasional in various meadow communities. Cooper.

ERIGERON PEREGRINUS (Pursh) Greene. Moraine meadow (52).

ERIGERON UNIFLORUS L. Station 41.

PETASITES FRIGIDA (L.) Fries. Moraine meadow (52); closed thicket (22).

PRENANTHES HASTATA (Less.) Jones. Station 5.

SENECIO PAUCIFLORUS FALLAX Greenm. Beach meadow (53).

SENECIO PSEUDO-ARNICA Less. Beach meadow (52).

SOLIDAGO LEPIDA DC. Moraine meadow (52).

SOLIDAGO MULTIRADIATA Ait. Occasional pioneer on moraine and gravels, becoming frequent in open thicket.

TARAXACUM LYRATUM (Ledeb.) DC. Point Gustavus, Coville and Kearney.

UNIVERSITY OF MINNESOTA
MINNEAPOLIS

# The effect of increased activities and change in mode of transportation upon the distribution of introduced species in the vicinity of Douglas Lake, Michigan[1]

HELEN R. COBURN AND DORIS L. DEAN

During the summer of 1914 a study of the introduced species of settled areas in the vicinity of Douglas Lake, Cheboygan County, Michigan, was made by Gleason and McFarland (1914) and continued by Gleason (1917). Since the time these two studies were made, automobile traffic to the lake has replaced horse drawn vehicles, most of the resorts have been extended and activities of the University Camps increased. To note the effect of these changes upon the introduced flora, studies were made during the summer of 1928 of introduced plants of Douglas Lake resorts, Northwoods Camp, the University of Michigan Engineers' Camp, the University Biological Station, and roads through uninhabited aspen growth (Gates, 1926). Special effort was made to include the identical areas studied by Gleason. Species listed in this study are those which are considered introduced according to Gray's Manual, together with certain weeds and such other species as are obviously introduced into this region.

## BIOLOGICAL STATION[2]

The two original laboratories were log buildings, a part of a construction camp that existed years before the Station was established. The introduced species listed by Gleason (1914) were believed to be chiefly a relic of the introduced vegetation of this construction camp. The Station has grown to a group of about fifty buildings, stretching for more than a quarter of a mile along the shore of Douglas Lake. Traffic to and from the Station was entirely by horse drawn vehicles until after 1914. Gradually automobiles have replaced the use of horses except during fall and winter, when traffic is exceedingly light. Omitting definite plantings, a total of 23 introduced species now occurs at the site of the Biological Station, two of which (*Conringia orientalis* and *Vaccaria vulgaris*) were brought in with seed bought for experimental animals in 1928.

[1] Contribution from the Biological Station of the University of Michigan. The studies were made under the direction and supervision of Professor F. C. Gates during the summer of 1928. Detailed lists for each locality studied are not included in this paper on account of space, but are deposited in the Biological Station Library.

[2] Since this paper was prepared, the Biological Station has been moved (in 1929) to the Camp Davis site, leaving only the two original log buildings.

### CAMP DAVIS[3]

On the southern shore of Douglas Lake adjacent to the Biological Station is Camp Davis. The camp is laid out with two rows of houses facing a central road. Brush and shrubs are well cleared out. The caretaker who lives in the camp keeps horses in an old barn. Here *Cerastium vulgatum*, *Poa pratensis*, *Poa compressa*, *Agrostis palustris*, and *Trifolium hybridum* grow on the dirt floor. Most of the 39 introduced plants were found along roadways near the barn and around the mess hall.

### ASPENS

The aspens are the vegetative cover of most of the area near the Biological Station. A few of the sandy roads wind irregularly through them, but there are no places of habitation. Three sets of studies were made which bring out the fact that introduced plants occur almost always only close to roads. A very short distance back from the road into the tree-covered ground sees the elimination of introduced flora. Three species (*Rumex acetosella*, *Poa compressa* and *Poa pratensis*) are the only ones likely to be any distance away from roads. The diminution of individual plants from the horse vehicle days is exceedingly apparent as one goes through the aspens, while the total number of species has been reduced from 21 to 17.

### BRYANT'S RESORT

The largest group of cottages of any resort at Douglas Lake is in the vicinity of Bryant's Hotel on the south shore of the lake. Auto traffic during the resort season has almost entirely replaced that of horses. In 1914, 24 species of introduced plants were listed from the yards surrounding the hotel and nearby cottages. This had increased in 1917 to 42 species. The number dropped one in 1928, though the species varied.

There was a marked difference in the number of plants near the cottages to the west and to the east of the hotel. Cottages to the west have been built more recently, tree growth is denser, the ground is covered with a mat of pine needles and here introduced plants were neither numerous in number nor species. Most of the cottages to the east of the hotel are in a more open situation and have been influenced longer by the introduced vegetation in the immediate vicinity of the hotel.

### NORTHWOODS CAMP

A few meters beyond the easternmost cottage of Bryant's resort is Wayside Inn, a summer house now used by Northwoods Camp established in 1925 on Bogardus Point. There were eight introduced species found

[3] Since 1930 the Biological Station operates on the former Camp Davis site.

here. In the yards of the buildings (one is over 25 years old) of Northwoods Camp and a grassy area adjacent, 18 introduced species occurred. Around the tents *Poa compressa*, *Poa pratensis* and *Lepidium virginicum* were the only introduced plants. The small number of introduced plants in the entire area owned by the camp might be explained by the constant cutting, raking, and burning of grass and weeds.

In 1926 a tennis court was made on the camp property near Bryant's Bog. Aspens and undergrowth had to be cleared for the court and clay hauled in for its surface, but at present five species occur around it (*Agrostis palustris*, *Lepidium virginicum*, *Poa compressa*, *Poa pratensis*, *Taraxacum vulgare*). Riding horses from Ingleside were brought to the camp two days a week during the camping season of 1926 and 1927. The season of 1928 was the first in which horses have been kept at Northwoods Camp. The constant use of all roads in the vicinity as bridle paths is destroying vegetation in the center of the road, yet in time may add new introduced species to these roadsides.

A total of 20 species are found at Wayside Inn, Northwoods Camp, and the tennis court, 19 of which occur at the Northwoods Camp.

### INDIAN HUT

A small clearing in the aspens near a bog about a quarter of a mile from Bryant's Hotel marks the site of an old Indian dwelling. There is no longer any trace of the hut, which for years stood as an adandoned dwelling. Eight species of introduced plants now occur in this area, while in 1914 the number was 15. *Rhus glabra* and *Rubus allegheniensis* from the aspens surrounding the clearing have spread rapidly in the past two or three years. As the clearing gives way to aspen growth, there may be a further reduction in the number of the introduced plants. The eight introduced species now present are: *Achillea millefolium*, *Agrostis palustris*, *Phleum pratense*, *Poa compressa*, *Poa pratensis*, *Rumex acetosella*, *Taraxacum vulgare*, and *Trifolium hybridum*.

### FAIRY ISLAND

Fairy Island extends for half a mile north from Bryant's Resort and is connected with the mainland by a narrow sand bar which is covered by water during the spring. Five cottages and an old ice house are the only buildings on the island. The stony beach on the west side of the island is wide enough at time of low water for the teams bringing building material to the island. In order to get from the mainland to the island, boats are used more frequently than the three paths extending the length of the island. A mixture of *Thuja*, *Pinus*, and *Betula* covers the island, and there is no other place in the vicinity of Douglas Lake where *Taxus* grows more

abundantly. The 23 introduced species are most numerous around the cottages at the northern end of the island, but are nowhere abundant.

### SILVER STRANDS

A half mile west from Ingleside is a group of less than a dozen summer cottages which for the seasons of 1927 and 1928 were unoccupied. Land to the north is part of a bog area which was burned in 1919 and 1923 and subsequent fires endangering the cottages have left this an unattractive part of the shore line. It was near a pig pen and neglected garden that most of the 17 introduced species were found in 1928.

### INGLESIDE

At Ingleside, one of the oldest resort areas on Douglas Lake, occurred a greater variety of introduced species than in any other settled area of the lake. The resort includes a group of cottages, farm buildings, and a hotel which is also the Post Office and store. More of the natural vegetation has been cleared for this resort than for Bryant's. Locations of most of the 64 introduced species in and near Ingleside were: a vegetable garden at the hotel; the road leading from the hotel behind the cottages to a farm house (the last building in this group); a lane from the farm house to the Ingleside road; and barnyard and chicken coop.

Twenty-nine species have been added since 1914, while seven found then were not found in 1928.

### NUTTING'S BAY

About half a mile east of Ingleside between Bentley's and a farm at Nutting's Bay is a group of cottages. The number of introduced species around them has been reduced since 1914 from 26 to 15. *Cerastium vulgatum* was the most abundant plant in this area. Boats are still used as means of transportation to Ingleside although the sandy road behind the cottages is used by autos. The 14 species lost were *Arenaria serpyllifolia*, *Bursa Bursa-pastoris*, *Chaetochloa viridis*, *Cirsium lanceolatum*, *Cynoglossum officinale*, *Lappula deflex*, *Nepeta cataria*, *Plantago lanceolata*, *Silene noctiflora*, *Sisymbrium officinale leiocarpum*, *Sisymbrium altissimum*, *Trifolium hybridum*, *Trifolium pratense*, and *Trifolium repens*, while *Cerastium vulgatum*, *Chenopodium album*, and *Euphorbia Cyparissias* had made their appearance.

For the past two or three seasons there has been no attempt to cultivate a farm at Nutting's Bay and no livestock has been kept at the farm. However, part of the farm home was occupied and there was a small neglected flower garden near the house. The number of introduced species in the barn yard, around the house and in the roadway (27) exceeds the num-

ber present at the cottages of Nutting's Bay. This difference may be expected, due to the previous cultivation of the farm and the former care of livestock on the farm.

### BENTLEY'S POINT

On a bluff northwest of Robert's Point is the Bentley summer home, built in 1925. No attempt has been made to preserve any of the natural flora. All underbrush has been cleared away, the bank stripped of vegetation and sodded, and most of the trees between the house and lake removed, leaving as the lawn, grasses common to aspen areas. Future plans for this land include extensive landscaping, but as yet there are only a few beds of cultivated flowers. Most of the 20 introduced species were found in and near these flower beds.

### ROBERT'S POINT

At Robert's Point (towards Ingleside from Kentucky Cottage) are two cottages where there is now no effort being made either to bring in cultivated plants or to preserve the natural vegetation. The yards at the rear of these cottages are low and rather moist. Most of the 15 introduced species were in the roadway and near the garage. *Alsine media* and *Cerastium vulgatum* were rather abundant near the porches and foundations of the cottages.

### KENTUCKY COTTAGE

A mile east from Ingleside and extending about a quarter of a mile along the shore is a group of five cottages where in 1914 there were only two cottages. The cottage farthest east has not been occupied for several seasons. Adjacent to it is Kentucky Cottage, one of the two original cottages of this group. In an attempt to make the yard surrounding Kentucky Cottage attractive there has been a conscious effort, while clearing underbrush, to disturb the natural vegetation as little as possible. There is no garden of cultivated flowers. *Chrysanthemum Leucanthemum*, transplanted near the porch and present in 1914, was the only introduced species that year. It has spread very little. *Sedum acre*, transplanted at the top of the bank near the path leading to the beach, is spreading down the bank. *Lepidium virginicum* and *Cerastium vulgatum* were found in pebbles left from a pile of stones brought to the cottage in 1927 for a fireplace. Near the same place was a small group of *Rudbeckia laciniata* which had been seen first in 1927 and was probably introduced in the material for the fireplace. *Lepidium virginicum* was present also among the stones of the path leading from the house to the beach. Near the ice house were *Rumex acetosella*, *Bursa Bursa-pastoris*, *Polygonum Convolvulus*, and *Plantago major*, which were found in no other place near the cottage.

Although Kentucky, Robert's, and Bentley cottages are fairly close to each other, three distinct attitudes are shown by the cottagers towards the natural vegetation: (1) an effort to preserve the natural flora, (2) an indifference towards preservation, (3) an effort to replace the natural vegetation with cultivated. For the twenty years Kentucky cottage has been occupied, there are fewer introduced plants than are found at Bentley's Point in the three years since the vegetation was disturbed. Of those at Kentucky several have been brought in just recently with material for a new fireplace and sawdust for the ice house. In 1914, introduced species in the roadway behind the cottage numbered 19. This has now been reduced to ten, but cottage, roadway, and ice house still have 19 introduced species.

### REESE'S CLEARING

Thirty-one introduced species occur in a clearing in Reese's Bog, where for a number of years there was a small dwelling. Gleason (1914) reported there were no introduced species in the clearing until 1912, and believed those had come in with packing material when a small cottage was built. The building was abandoned a few years ago and now no part of the building remains.

### NEW REESE'S BOG ROAD

In an attempt to extend the resort area at the north end of Burt Lake, a road was begun in 1926 parallel to and not far back from the beach. Clearing for the new road extended through the bog for more than a half mile on each side of the road to Burt Lake. Where sand and clay had been hauled in to fill the spaces between the felled trees used as foundation of the new roadway, 19 introduced plants were found. By 1928 the sand and clay of the abandoned road had settled sufficiently so that in places the road bed was wet and some of the bog plants were again becoming established. Introduced species, particularly *Rumex acetosella*, *Verbascum thapsus*, and *Taraxacum vulgare*, were abundant in the dry, sandy places.

### PELLSTON

At a mill yard at Pellston, a few miles west from Douglas Lake, the list of 58 species included a greater variety of introduced plants than were recorded for most other locations in the vicinity of the lake, although the individual species were neither abundant nor evenly distributed.

Table I was compiled, using all the locations studied in 1928 and comparing with these (where the same areas were mentioned) the number of species recorded by Gleason or McFarland in 1914 and 1917. It may be noted that where the number of introduced species of 1928 exceeds that of

other years, the areas are inhabited and the land is either partly cultivated, or there has been an increase in the number of buildings.

Where the area has been abandoned, the number of introduced species diminishes through lack of disturbance due either to cultivation or livestock. Most noteworthy however is the diminution of introduced species in and near the roads through the aspens, in spite of the very great increase in amount of travel now compared with the day of the horse. Quantitatively the diminution is much greater than the reduced number of species on the list would indicate.

TABLE 1

*Number of introduced species recorded by Gleason and McFarland in 1914; by Gleason in 1917, and by Coburn and Dean in 1928*

| Locations | 1914 | 1917 | 1928 |
|---|---|---|---|
| Douglas Lake | | | |
| 1. Biological Station* | 21 | — | 23 |
| 2. Camp Davis* | — | — | 39 |
| 3. Aspens | 21 | 14 | 17 |
| 4. Bryant's | | | |
| (a) Hotel and Cottages* | 24 | 42 | 41 |
| (b) Northwoods Camp* | — | — | 20 |
| (c) Indian Hut | 15 | 9 | 8 |
| (d) Fairy Island* | — | — | 23 |
| 5. Silver Strand | — | — | 17 |
| 6. Ingleside* | 42 | — | 64 |
| 7. Nutting's Bay* | 26 | — | 15 |
| 8. Nutting's Bay Farmyard | — | — | 27 |
| 9. Bentley's* | — | — | 20 |
| 10. Robert's Point* | 20 | — | 15 |
| 11. Kentucky Cottage and nearby road* | 19 | — | 19 |
| Burt Lake | | | |
| 12. Reese's Clearing | 24 | 32 | 31 |
| 13. New Reese's Bog Road | — | — | 19 |
| Pellston | | | |
| 14. Millyard* | — | — | 58 |

* Inhabited.

## SUMMARY

1. On roads through aspen growth, in the vicinity of Douglas Lake, Cheboygan County, Michigan, there has been a noteworthy reduction in number of introduced species in the dozen years since auto traffic has replaced horse-drawn traffic.

2. There is a diminution in number of introduced species with increasing distance from roads through the aspens.

3. Construction of new buildings, bringing a greater number of people to the lake, has been accompanied by an increase of introduced vegetation in the inhabited areas. This, however, has not increased the introduced element along roads.

4. Areas abandoned show varying reduction in the number of introduced species.

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## INDEX TO AMERICAN BOTANICAL LITERATURE
### 1927–1930

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the work America being used in the broadest sense.

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